Report of the Working Group on Fisheries Ecology

Andrey Dolgov, Jim Elkis, Micholas Dulvy, and Geir Huse

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Report of the Working Group on Fish Ecology (WGFE)

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International Council for the Exploration of the Sea
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H. C. Andersens Boulevard 44–46
DK-1553 Copenhagen V
Denmark
Telephone (+45) 33 38 67 00
Telefax (+45) 33 93 42 15
www.ices.dk
info@ices.dk

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Contents

Executive Summary

In 2009, WGFE (Working Group on Fish Ecology, D. W. Kulka, Chair) met at ICES Headquarters from 26-30 October. Sixteen participants from eight countries (Annex 3) addressed six Terms of Reference (ToR – refer to Annex 1). The work of the group was accomplished by subgroups assigned to each ToR and the report is structured as a single chapter for each ToR. Below, the results linked to the Science Plan (Annex 2).

ToR a (Science Plan links: 2, 3, 7, 8, 13)

It was demonstrated that the Large Fish Indicator could be modelled using a subset of species from a full demersal assemblage, thus the LFI is not a true community indicator.

A satisfactory fit to North Sea landings, recruits, stock biomass, population length distributions and diet data was achieved using FishSUMS, a length-structured multispecies fish community model. Future work should incorporate recruitment variability and environmental drivers.

Work on recovery of the North Sea demersal fish community to the EcoQO (fish community target state indicative of health) used a size-based model to explore tradeoffs between fisheries and conservation objectives and examined how state indicators respond to fishing pressure. Future work could include the implementation of observation and process error into the modelling frameworks, spatial processes, comparisons across ecosystems and/or spatially distinct areas within ecosystems.

ToR b (Science Plan links: 2, 3, 13, 14)

Of 15 metrics examined to act as surveillance indicators of change in the "health" of the North Sea's demersal fish community, several were found to vary independently. The attributes condense down to the number of individuals and species in the community and relative distribution of individuals among species. Variation in the community structure attributes either influenced or was influenced by variation in the size of individuals and life-history characteristics.

ToR c (Science Plan links: 8, 13, 14)

Spatial analysis provides a powerful suite of tools for interpretation and analysis of spatially explicit data, enabling testing of predictions and display of multi-dimensional and derived statistics from imperfect and often noisy spatial information. Examples in the report illustrate how spatial modelling can be used to support management strategies or represent population metrics spatially.

Knowledge on the quality of new habitat arising from range changes is important for studying the impact of climate induced distributional changes. Bioclimate envelope modelling was highlighted as one of the few available quantitative tools for making predictions of habitat availability and for predicting potential ecological changes resulting from distribution shifts.

The response of marine communities to one or more drivers depends on the strength of the drivers, the environment in which the community resides and the identity, abundance, and dynamics of the community components. Self-Organising Maps (SOMs) have been developed as a tool to identify spatial locations where similar responses have taken place. Current research is combining data from satellite remote-sensing, physical *in situ* oceanographic surveys, habitat classification and fisheries monitoring surveys.

ToR d (Science Plan links: 8, 14)

Residuals in the occupancy-abundance relationships of Georges Bank fish showed a breakpoint corresponding to a large decrease in occupancy in 1972 when fishing effort greatly increased. That year forward, species dominance increased and evenness decreased circumstance where a community could become more vulnerable to perturbation such as fishing.

A comparison of abundance-occupancy relationships and life history characteristics for species common to NW and NE Atlantic were examined. There was a significant difference in 15 of 23 species between the two areas.

Tor e (Science Plan links: 6)

As a signatory of the Convention on the Conservation of European Wildlife and Natural Habitats, member states of the EU prepared a list of Sites of Community Importance. Member States are required to maintain or restore those natural habitats including fauna and flora. In considering this ToR, the working group concluded that it would not be possible for ICES to provide comprehensive lists of fish species associated with the broad habitat classifications. Instead, WGFE has summarised available information on fish assemblages for each of the three habitat types.

ToR f (Science Plan links: 1, 2, 11)

WGFE prepared two chapters as input to an ICES Position Paper on Climate Change. The first focused on temperature induced changes in fish species, depth and latitudinal shifts, range extensions/retractions influx and migrations, growth, maturation and recruitment and interactive effects of climate and fisheries. Suggested future research directions included: disentangling climate variability from climate change; physiological processes underlying climate-fish relations; differences in vulnerability of species and life-stages; (dis)similarity in species responses; interaction between climate change and fisheries effects; effects of climate change on fisheries; and modelling techniques for synergistic top-down (fisheries) and bottom-up (climate) effects. The second chapter dealt with sensitivity of marine ecosystems to climate variability and regime shifts. Key parameters to investigate include: the influence of ecosystem complexity; sensitivity of populations to seasonal temperature extremes which would increase with climate change; the influence of dispersal capabilities, habitat, life-history characteristics and dietary preferences on sensitivity; the balance between fixed genetic factors vs. phenotypic plastic responses; and the adaptability of socially and culturally mediated behaviours such as migrations.

Demersal fish community structure in the northeast Atlantic has not undergone the degree of change that occurred in the northwest Atlantic. Changes in the northeast comprise distributional shifts rather than full scale replacement of species assemblages. On the other hand, there was an abrupt shift in the demersal community of the northwest Atlantic where the majority of demersal fish declined synchronously replaced in dominance in the ecosystem by shrimp and crab. Juxtaposing these two situations may lend some insights into the concept of regime shifts and the sensitivity of different communities and ecosystems. Future research directions should include the examination of changes in fish communities by latitude and importance of diversity and production in terms of system resilience.

1 Introduction

1.1 Terms of reference for 2009

Refer to Annex 1 and at the head of each chapter.

1.2 Participants

Ken Haste Andersen (AQUA, Denmark)
Julia Blanchard (CEFAS, England)
Tom Blasdale (JNCC, Scotland)
Daniel Duplisea (DFO, Canada)
Jim Ellis (CEFAS, England, via correspondence, Section 6)
Mike Frisk (SBU, USA)
Simon P.R. Greenstreet (FRS, Scotland)
Emma Guirey (FRS, Scotland)
Ralf van Hal (IMARES, Netherlands)
Dave Kulka (DFO, Canada)
Anna Rindorf (AQUA, Denmark)
Marie Louise Schrøter (AQUA, Denmark)
Anne Sell (ISF, Germany)
Stephen Simpson (UB, England)
Lorna Teal (WRL, Netherlands)
Verena Trenkel (IFREMER, France)

Full contact details of participants are provided in Annex 1.

1.3 Background

The rationale behind the formation of The Working Group on Fish Ecology (WGFE) in 2003 was to support ICES on issues of fish community metrics and to provide advice on threatened marine fish. Until 2002, fish community issues were considered by WGECO, but as the demands on that WG increased, the establishment of WGFE enabled a more focused consideration of fish community issues.

WGFE has previously met before the Working Group on the Ecosystem Effects of Fishing Activities (WGECO) for which WGFE's report was anticipated for that group to complete its work. WGECO has traditionally commented on the report of WGFE and asked specific pieces of analysis to be performed at its next meeting thus providing a clear linkage between the more pure science products of WGFE and the need for advice to inform policy considered by WGECO. 2009 represents the first year that WGFE met after WGECO.

WGFE has addressed issues on non-commercial fish species, including species of conservation importance, fish communities and assemblages, impacts of climate change on fish communities and other aspects of fish ecology (e.g. feeding habits and prey rations, habitat requirements), to support ICES advice in areas related to ecosystems, biodiversity, conservation and climate change. In addition to supporting scientific advice, WGFE is a group that can incorporate and germinate scientific ideas related to methodological development and ecological synthesis; thus, WGFE has become a point of initiation into ICES for new researchers and researchers who have not before been involved in practical applications of their science.

With the recent transformation in the ICES structure, WGFE is now guided by the ICES Science Plan (2009–2013). The parent group is SSGEF (SCICOM Steering Group on Ecosystem Function), one of five groups reporting to Science Committee. As well, SGCC (Study Group on Climate change) referred a request for information on climate change for the ICES Position Paper, Science Strategic Initiative on Climate Change (ToR f, Annex 1) as it relates to fish (refer to Annex 6 for further linkages within ICES). The mandate of WGFE is designed to address many of the sixteen "high priority research topics" that the Science Committee formulated as the basis for the Science Plan. The WG focuses primarily on those topics that fall under the thematic area entitled "*Understanding Ecosystem Functioning*" but also addresses topics under "*Understanding Interactions of Human Activities with Ecosystems*" and to a lesser extent under "*Development of options for sustainable use of ecosystems*". This year, the work was focused on metrics, modelling, distributional relationships of fish and their association with various habitat components. Some focus was given to the affects of climate change and it is expected that this will be a focus for future work of the group.

The group now has a more focused mandate than in the past under the new ICES structure. Future work of WGFE will be closely aligned with the Plan and SSGEF.

1.4 References

ICES. 2003. Report of the Working Group on Fish Ecology (WGFE). ICES CM 2003/G:04; 113 pp.

ICES. 2004. Report of the Working Group on Fish Ecology (WGFE). ICES CM 2004/G:09; 257 pp.

ICES. 2005. Report of the Working Group on Fish Ecology (WGFE), 21–26 February 2005, Santander, Spain. ICES CM 2005/G:05. 220 pp.

ICES. 2006. Report of the Working Group on Fish Ecology (WGFE), 13–17 March 2006, ICES Headquarters, Copenhagen. ICES CM 2006/LRC:06. 154 pp.

ICES. 2007. Report of the Working Group on Fish Ecology (WGFE), 5–9 March 2007, Nantes, France. ICES CM 2007/LRC:03. 217 pp.

ICES. 2008. Report of the Working Group on Fish Ecology (WGFE). 3–7 March 2008, ICES Headquarters, Copenhagen. ICES CM 2008/LRC:04. 119 pp.

2 Modelling approaches for projecting decline and recovery of fish community state metrics in response to fishing and other pressures

ToR a) Explore the utility of a variety of modelling approaches for projecting, decline and recovery of fish community metrics to target indicators of state (e.g. EcoQOs) in response to fishing pressure and environmental variability.

i. Explore the role of uncertainty (e.g. model, process, estimation, observation uncertainty) in these models in the context of probability of achieving targets.
ii. Evaluate the potential to and implications of fitting these models to data.
iii. Explore and update the list of modelling approaches from WGFE 2008, including qualitative modelling.
iv. Apply models to the North Sea EcoQO.

2.1 Introduction

2.1.1 Background

The Marine Strategy Framework Directive (MSFD) requires Good Environmental Status (GES) for ecosystem components and attributes (*e.g.* populations, communities, foodwebs, seabed habitats and biodiversity). Management towards GES will typically use a Pressure-State-Response framework. Fish community metrics, or indicators, give information about the state of the fish community. A particular level or range of the indicator is identified as a "good" state for the system. Management advice is then given as to how to achieve this level of the indicator by managing the pressures on the system. Some examples of proposed indicators for the fish community include diversity indicators such as species richness and evenness, life-history characteristics like mean asymptotic length or length at maturity, total biomass or abundance, trophic dynamic indicators and size-based indicators such as the Large Fish Indicator (proportion of fish by weight larger than 40 cm in length), mean fish size and slope of the community size spectrum (Rochet and Trenkel 2003).

The Pressure-State-Response framework requires understanding of how "pressure" relates to "state", or the proxy for state. In other words, we must know how the indicators are affected by the pressure imparted on the system. Empirical analysis can be used to build statistical models between pressure and state. However, to gain understanding about the processes operating, and in order to make predictions, fish community models are required. These models are needed to answer questions such as the following:

- What should reference or desirable levels be for indicators?
- How do indicators respond to fishing and other pressures, anthropogenic and otherwise?
- How can we balance the need for a sustainable (high yield) fishery and a sustainable ecosystem, functioning appropriately? For example, can we simultaneously achieve GES for the fish community and Maximum Sustainable Yield for all commercial species?
- Do the indicators make sense? For example, is there a bijection between state and indicator or could we have multiple (possibly undesirable) states giving the same indicator value?
- Can indicators be used in a traditional PSR framework? i.e. can models inform what the management response should be to reach a desired state?

Several models exist which can be used for the evaluation and development of ecosystem and fish community metrics (see reviews by Plagányi, 2007 and Rose and Sable, 2009) and a review of candidate models for application to the North Sea Large Fish Indicator (LFI) can also be found in ICES (2008). Suitable models for evaluating fish community indicators must represent the key processes operating on the fish community and interacting components and must quantify the pressure exerted upon the system. To evaluate size-based indicators, size-structure must be included in the model. Multispecies size-structured models are ideally placed for this.

2.1.2 Application of models to the North Sea fish community

In this Chapter the utility of typical multispecies models in application to fish community indicators is explored.

In Section 2.2, it is shown that the Large Fish Indicator may be modelled using a partial ecosystem model, *i.e.* without explicitly representing all of the species in the North Sea fish community.

In Sections 2.3 and 2.4, two quantitative size-structured multispecies models are applied to the North Sea fish community: FishSUMS, a Fish community model developed by Strathclyde University and Marine Scotland, and a multispecies size-spectrum model developed under the EU project "Indicators for ecosystem-based fisheries management in Europe" (IMAGE). Both are multispecies, length-structured models that have aspects in common with the size-structured multispecies model of Hall *et al*. (2006). Although these models are quite similar, some of the key assumptions and processes differ. FishSUMS incorporates physiological recruitment, with explicit representation of eggs and larvae, but uses determinant growth. The multispecies size spectrum model incorporates food-dependent energy allocation to growth.

This work explores aspects of data fitting and uncertainty, which are summarized in Section 2.5.

Finally, recommendations are given in Section 2.6.

2.2 Modelling the LFI with a partial community

Work was carried out establish whether the LFI can be modelled using a subset of species from the full demersal assemblage sampled by the IBTS. In other words, can partial ecosystem/minimum realistic models model the LFI?

The LFI is calculated from IBTS Quarter 1 data. Over 95 demersal species are sampled by the IBTS (Fraser *et al*., 2007). In contrast, existing multispecies fish models typically represent of order ten species, focusing on the more dominant, well-studied and commercially important. It is hoped that these models can be used in hindcasting, predicting and understanding trends in the LFI. Therefore, it must be emphasized to establish whether the LFI calculated using a subset of species is related to the indicator calculated from the full assemblage sampled by the IBTS.

Here, the LFI is re-calculated using two subsets of the full surveyed assemblage:

1. Cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*), ling (*Molva molva*), starry ray (*Amblyraja radiata*), monkfish (*Lophuis sp.*), common dab (*Limanada limanda*), plaice (*Pleuronectes platessa*), lemon sole (*Microstomus kitt*), long-rough dab (*Hippoglossoides platessoides*), poor cod (*Trisopterus minutus*), Norway pout (*Trisopterus esmarki*) and grey gurnard (*Eutrigla gurnardus*). These are the 14 demersal species making up over 95% of the total biomass and previously identified as a goal species assemblage for modelling the LFI (ICES, 2008).
2. Cod, haddock, whiting, common dab, Norway pout and grey gurnard. These are the demersal species currently represented in the FishSUMS model (see Section 2.3).

Figure 2.1 shows the time-series of the LFI calculated using the full assemblage, subset 1 and subset 2: $\mathrm{LFI}_{\mathrm{full}}$, LFI_{1} and LFI_{2}, respectively. The values for each time-series are plotted against each other in the bottom scatterplots. The time-series of $\mathrm{LFI}_{\mathrm{full}}$ and LFI_{1} are closely aligned, with all peaks and troughs simultaneous. LFI_{1} is consistently lower than $\mathrm{LFI}_{\mathrm{full}}$. The maximum deviation between the two series is 0.0323, or 20%, in 1991. In all other years, the deviation is less than 10%. The Pearson's correlation coefficient for the two samples is $r=0.995$. The time-series of $\mathrm{LFI}_{\mathrm{full}}$ and LFI_{2} are also closely aligned. LFI_{2} is less than $\mathrm{LFI}_{\mathrm{full}}$ in every year. The deviation is greater, with a maximum deviation in 2003 of 66%. However, the two series are closely linearly correlated with $r=0.962$.

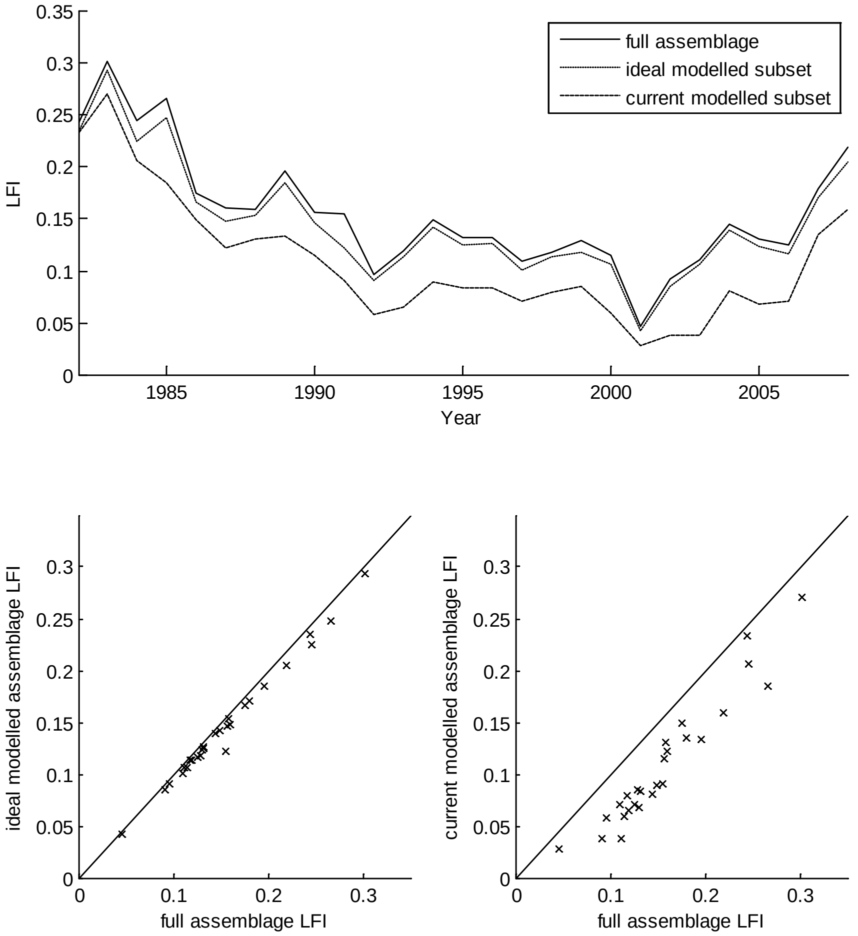


Figure 2.1. The Large Fish Indicator calculated from Q1 IBTS data from 1982 to 2008 for (1) all demersal species caught in the survey, (2) the ideal modelled assemblage and (3) the set of species currently represented in the model (see Section X). Bottom panel compares the time-series. Solid lines in these plots indicate the line with slope 1.

This work shows that in theory it is not necessary to explicitly represent the full set of species caught in the IBTS to model the LFI. This is an encouraging result in support of partial ecosystem (or Minimum Realistic) modelling, because for many species – non-assessed or little-studied species, in particular – it is difficult to obtain the data necessary for model parameterization. On the other hand, these results suggest that the LFI is not a true community indicator, as it can be modelled using only a small set of commercial fish species.

Of course, results will depend on which species are excluded; an extreme example would be the omission of all species with maximum length greater than 40 cm. Previous work (ICES 2009), breaking down the time-series of small and large fish biomass into species indicates that cod, Norway pout, haddock and saithe are particularly important drivers of the LFI.

2.3 Modelling retrospective time-series in the North Sea fish community with FishSUMS

2.3.1 Introduction

FishSUMS is a length-structured multispecies fish community model developed for the purpose of hypothesis testing in ecosystem-based fisheries management. A particular motivation has been the development of a tool for modelling past and future trends in the Large Fish Indicator (LFI). A full description of FishSUMS is available in (Speirs *et al.*, 2009). We provide a summary here.

The model represents key species as length-structured. The current model version has evolved from a cod-centric version that has been used to test hypotheses about the recovery (or otherwise) of cod stocks in the North Sea with respect to the interactions between cod and its main prey and predators. Hence, species currently represented are cod, haddock, whiting, common dab, Norway pout, herring, sandeel, Nephrops and grey gurnard. These are modelled in discrete length-classes from eggs to maximum adult length assuming von Bertalanffy growth. At each model time-step, a fraction of individuals of each species- and length-class survive and a fraction of those grow to the next size class. Per capita fecundity is a species-dependent function of length. Egg production over a time-step is placed in a discrete egg class and the fraction of eggs surviving background and predation mortality progress to the first hatched length-class. The total food intake of each predator class is removed from its prey classes in proportion to prey abundance, weighted by a predator species dependent length preference. Survival and growth through the length-classes is, therefore, a function of background mortality, length-, species- and time-dependent fishing mortality and multispecies predation mortality; the latter depending dynamically on the abundance of predators. Zooplankton, benthos and small prey fish are modelled as size-spectra, in which each size class is modelled by chemostat dynamics subject to predation by size-structured species.

2.3.2 Current model overview

The development of FishSUMS is documented in ICES (2008), Guirey *et al.* (2008) and ICES (2009). The latter summarizes some of the problems encountered during model development. These include difficulties with stability and coexistence of species populations, lack of data for robust model parameterization, questions about where and whether density dependency acts as controls on populations and how to appropriately represent recruitment.

In order to circumvent some of these difficulties, a simplified version of FishSUMS was created. This enabled the project to move forward in fitting the model to North Sea data and making a first attempt at modelling trends in the LFI. The current version of the model represents a compromise between a fully flexible dynamic model representing all processes operating on the fish community and a hypothesis-testing, simplified model that is more "pinned-down" to data. Key aspects are summarized below.

- The model differs from its original form in being top–down controlled; as fish grow along a von Bertalanffy trajectory, with variability of size-at-age, they are assumed to meet their requirements for maintenance, growth and egg production. Growth is not food dependent. This assumes that food is not limiting to growth and corresponds to the "efficient predator" assumption employed by previous authors (*e.g.* Hall *et al.*, 2006; Butterworth and Plagányi, 2004). The functions previously used to represent food-dependent growth; mortality and reproduction have been "turned off" in the model by setting their minimum and maximum rates to be equal. This has allowed construction of a stable model with coexistence of multiple species. However, it is recognized that food-dependent growth is likely to be a more scientifically robust assumption, and that at least some bottom-up control is likely to be exerted in real world ecosystem. This will be re-examined in future work. A generic density-dependence term acts as a proxy for population control.

- Unlike most other multispecies models, recruitment is not generated by fixed stock–recruit relationships; egg production, mortality from predation, hatching and growth are modelled explicitly
- The model deals effectively with multispecies predation effects. In other words, "natural" mortality is not assumed to be fixed. Additionally, the explicit representation of eggs and larvae allows for predation on early life stages.
- The model is fit to multiple North Sea datasets.
- The model was adapted to include a routine for calculating the LFI in Quarter 1 for all years from 1982. The IBTS survey was emulated by applying length- and species-dependent trawl selectivity coefficients to the numbers output by the model. These empirically-derived selectivities are taken from the analysis by Fraser *et al.* 2007, comparing MSVPA output with IBTS data for the years 1998 to 2004. The LFI is then calculated by summing the selectivity-corrected biomass of demersal species above and below the 40 cm threshold. It has been shown in Section 2 (see Figure 2.1) that the LFI calculated from data using this subset of species is closely related to the full-assemblage empirical LFI.

2.3.3 Parameters, drivers, model runs and data fitting

Where available, life-history parameters from each species were taken from FishBase (Froese and Pauly, 2009). Diet species were taken from the 1981 Year of the Stomach data (Greenstreet 1996) and a recent North Sea study by Fraser (2009). Egg and larvae parameters came from Munk and Nielsen (2005). Fecundity data were taken from FishBase and Heath (2007). Parameters not obtainable from the literature or subject to much uncertainty were treated as tuning variables.

The model was driven by yearly fishing mortality, F, at age by species. These values were taken from the ICES WGNSSK 2007 report for cod, haddock, whiting, Norway pout, sandeel, herring and Nephrops. The year of first assessment varies by species; herring are assessed from 1960, cod and haddock from 1963, whiting from 1980 and sandeel and Norway pout from 1983. Estimates of F from 1920 by Pope (1996) were used to extend the cod, haddock and whiting time-series back to 1960. Landings were used to extend the time-series for Norway pout and sandeel, for which a significant relationship between landings and fishing mortality was shown. Common dab and grey gurnard are not assessed. A length-based F estimate for these species by Pope (2000), combined with landings data, was used to generate a rough time-series of F for these species. Hence, the level of confidence we have in F varies with species and year. Because the model is length-based, F at age then had to be converted to F at length.

The model was run for an initial 100 year spin-up with zero fishing mortality, until equilibrium was reached for all species, and a subsequent 100 year run with F as in 1960. Thereafter, the model was run with the F time-series from 1960 to 2006.

The model was tuned by hand to get the best fit, by eye, to five datasets:

1) Yearly total-stock biomass (TSB) in Q1 from ICES assessments (ICES, 2007).
2) Recruit numbers (ICES, 2007).
3) Normalised population length distributions from the 1991 IBTS.
4) Stomach content data by length from the 1981 Year of the Stomach (Greenstreet 1996). Grey gurnard stomach content data came from Mackinson and Daskalov (2007).
5) Yearly ICES assessed landings (ICES, 2007).

2.3.4 Results

Figures 2.2 to 2.7 show observed and modelled TSB, recruitment, length distributions, diet and landings, respectively. A reasonable fit to the general trends is obtained for all datasets. The fit to diet data are remarkably close. Here, we focus on the LFI results.

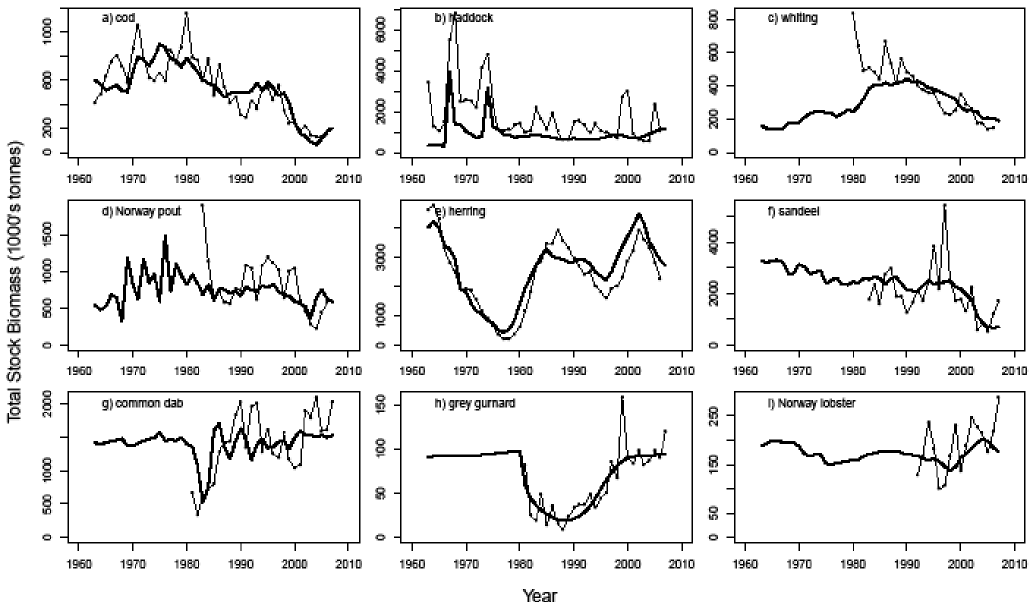


Figure 2.2. Time series of modelled (thick line) and observed (thin line with points) total-stock biomass (TSB) of all the length-structured species in the model. In this model variant, the recruitment of herring and sandeel has been reduced post-2001, and haddock recruitment has been enhanced in two pulses in 1966 and 1973.

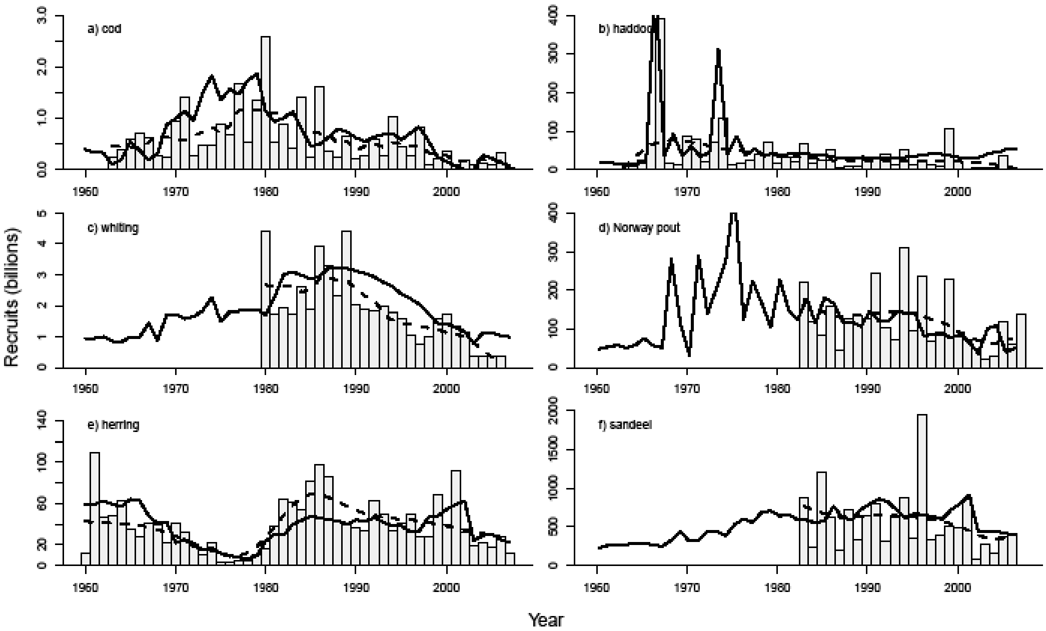


Figure 2.3. Time series of modelled (line) and observed (bars) recruitment for the ICES assessed fish species. The dotted line is a smooth through the observations using Friedman's (1984) "super-smoother" implemented in R.

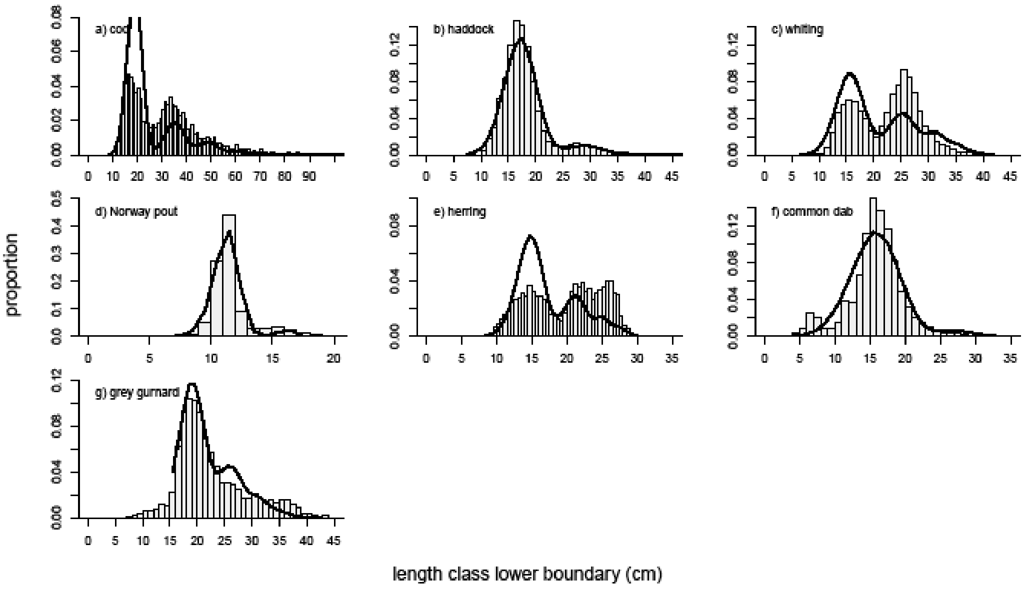


Figure 2.4. Normalised modelled and observed length distributions for cod, haddock, whiting, Norway pout, herring, common dab and grey gurnard in Q1 of 1991. The histogram bars give the proportion of the population in length classes derived from the IBTS in the North Sea. Solid bar gives corresponding model output.

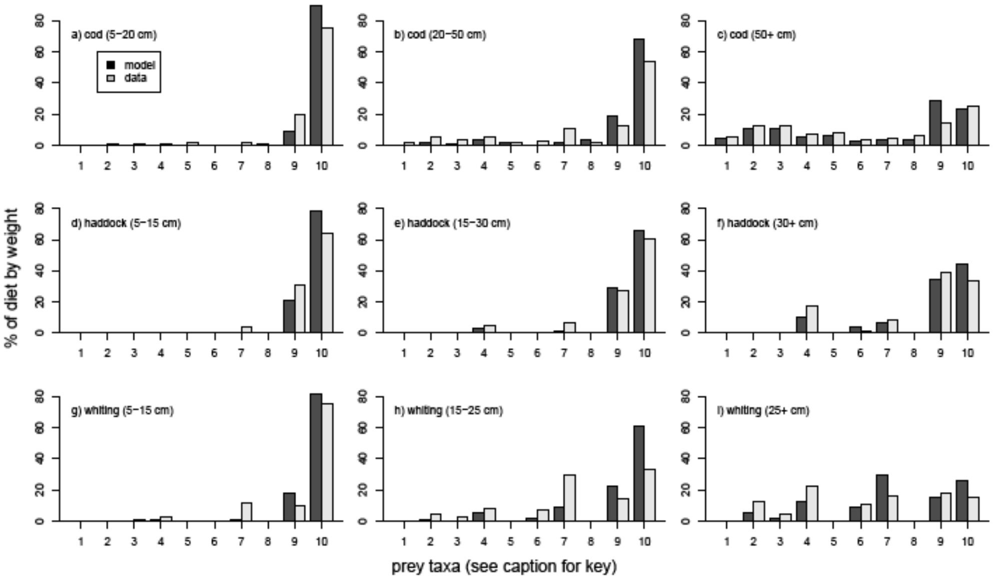


Figure 2.5. Modelled and observed diets (% by weight) of various size categories of the demersal piscivores, cod, haddock and whiting, in Q1 of 1981. Numbers on the x-axis give prey species: 1=cod, 2=haddock, 3=whiting, 4=Norway pout, 5=dab, 6=herring, 7=sandeel, 8=Nephrops, 9=other fish, 10=benthos. The observations are from Greenstreet (1996).

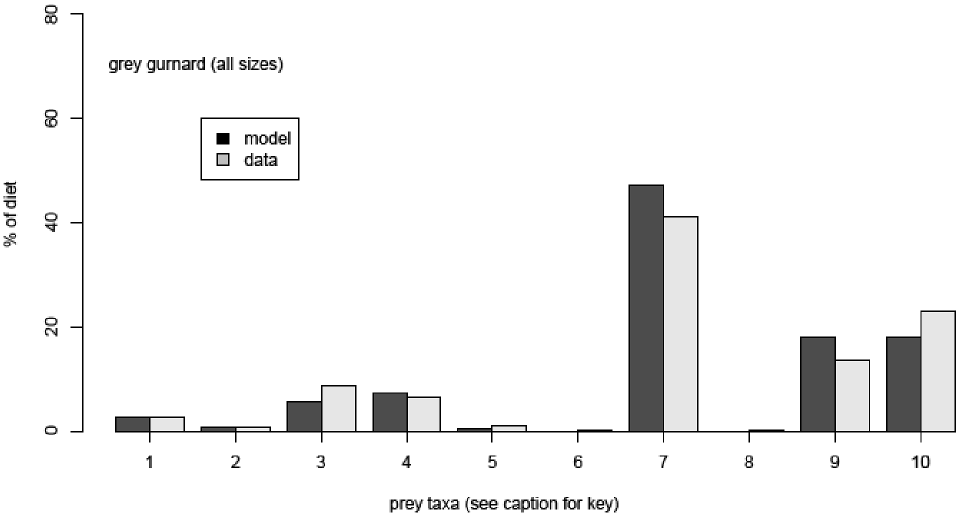


Figure 2.6. Modelled and observed diets (% by weight) of grey gurnard (all sizes) in Q1 in 1991, x-axis numbers as in Figure 2.5. The observations are taken from Mackinson and Daskalov (2007).

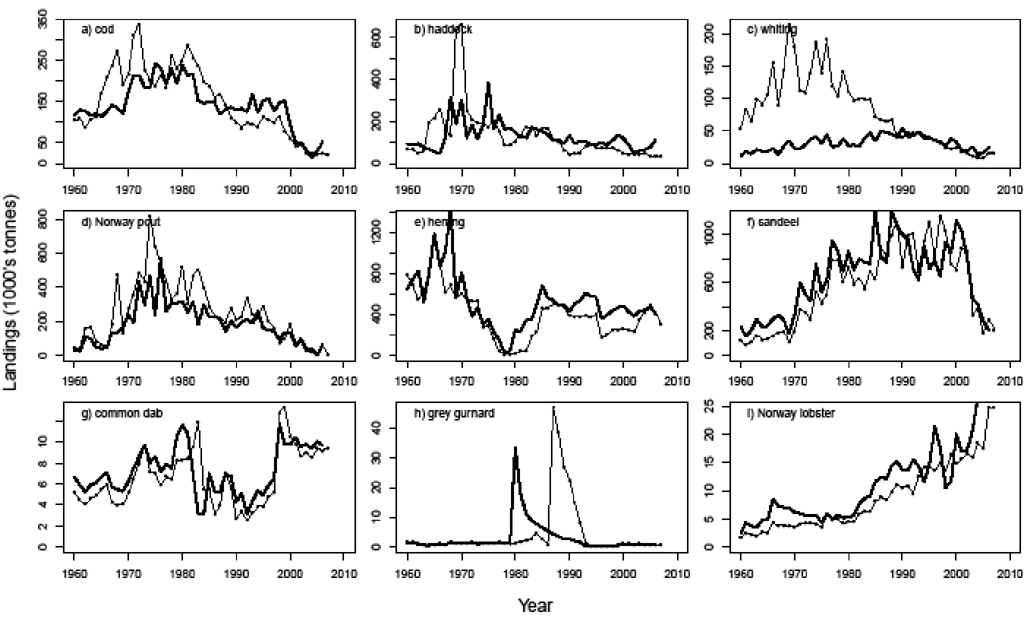


Figure 2.7. Time series of modelled (thick line) and observed (thin line with points) landings of all the length-structured species included in the model.

Figure 2.8 shows the LFI time-series calculated from the model. The top and bottom panels compare the model LFI with the IBTS-derived LFI using the whole demersal fish assemblage and the subset of species represented in the model, respectively. The right panels compare the model and data LFI values in each year.

The model and data LFI are highly correlated, with correlation coefficients of R^2=0.69 and R^2=0.78 (2 s.f.) for the full and modelled assemblage, respectively (p values < 0.001). The best fit linear relationship between the data LFI using the modelled assemblage and the model output LFI has slope 0.3 and intercept 0.0227. In general, the model output LFI is too low. The direction of change in the LFI between years was examined by subtracting LFI(y-1) from LFI(y) for each year *y* from 1983 to 2006.

The model output had the correct direction of change (increase or decrease between years) in 14 out of 24 years. The two largest deviations between the model and data LFI occur in 1992 to 1993 and 2003 to 2004.

In 1992/3, the model LFI has an increase where the data LFI has a decrease. A breakdown of the biomass of fish below and above the 40 cm threshold by species reveals the reason for this: the model fails to reproduce the peak in Norway pout and small haddock abundance seen in IBTS data. Of the species represented in this configuration of the model, Norway pout and haddock are the key drivers of the biomass of "small" fish (see ICES WGECO 2009 report, page 153).

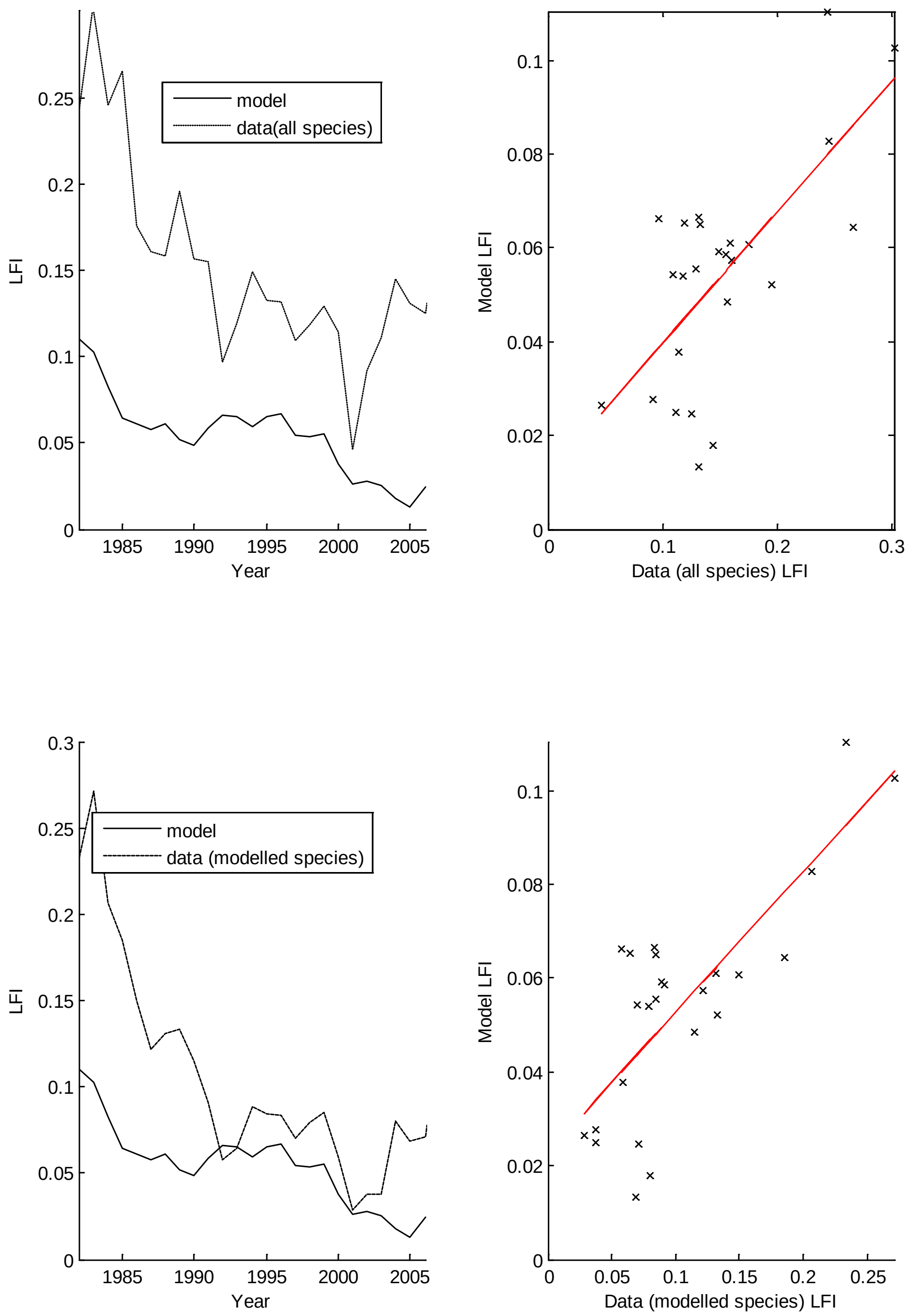


Figure 2.8. Time series of LFI calculated from IBTS and model data (left). Data LFI is calculated from the whole IBTS-sampled assemblage (top) and modelled species assemblage (bottom). Right panels show the data and model LFI in each year plotted against each other with line of best fit in red.

In 2003/4, the model LFI has a peak where the data LFI is seen to decrease. Similar analyses show that this is as a consequence of the failure of the model to capture a peak in large cod biomass seen in the IBTS data. Of the modelled species, cod is the key driver of "large" fish biomass (see ICES WGECO report 2009, page 153), with order of magnitude higher biomass compared with the "large" fish biomass of other species. Hence, failure to capture trends in the biomass and length distribution of cod prevents the model from capturing trends in the LFI.

2.3.5 Discussion

FishSUMS has been fit to a comprehensive set of North Sea data. This exercise has shown that it is possible, with a fairly simple multispecies fish model, to simultaneously achieve a satisfactory fit to landings, recruits, stock biomass, population length distributions and diet data. We also found that a close fit to the data could not be obtained when multispecies interactions were switched off in the model (see Speirs, 2009).

The results presented here show that the FishSUMS model is capable of reproducing trends in the LFI with a minimal set of key species. The model LFI and data LFI, calculated on the subset of species represented in the model, are remarkably well correlated. Despite this, the inclusion of more species would eliminate the need for this extra step between the model and IBTS LFI values. Key species not currently represented in the model, and shown by WGECO (see 2009 report, page 153) to contribute significantly to the "large fish" biomass, are saithe, pollack, ling and ray species. Saithe, as an assessed species, could easily be incorporated into the modelled assemblage. Non-assessed species are problematic; it is difficult to obtain parameter values and driving data. Additionally, if we can use a very minimal set of species to model the LFI, does that imply that the LFI is not a true community indicator?

The model currently has no representation of recruitment variability or environmental drivers. Consequently, it fails to generate the huge variability of recruitment for species such as haddock and cannot be expected to model the variability around the trend in "small fish" biomass. Future work will look at driving the model with a time-series of recruitment, where available, to see how much "better" the model can do at matching past trends. It is remarkable how well the model captures the past trend in the LFI even without the inclusion of recruitment variability, but it will certainly be necessary to consider recruitment variability when the model is used to make predictions.

The current implementation of the model applies empirically-derived catchability coefficients (Fraser *et al*. 2007) to the model output to simulate the IBTS survey. Fraser *et al*. (2007) discuss various problematic aspects of their study that may affect use of these coefficients here. For example, the study neglects spatial or inter-year variability of catchability, does not utilize data for the full length range of each fish species and is biased towards the southern North Sea. Also, their catchabilities are calculated using Q3 data and the LFI is calculated using Q1 data. If the selectivity coefficients applied here are inappropriate then unnecessary errors will be introduced into the LFI calculations. Alternative (*e.g.* pure length-based) schemes could be implemented to study the sensitivity of results to the choice of catchability coefficients.

The essential remit of this modelling work is to make predictions about the LFI under different fishing and climate scenarios. Although the model successfully captures past trends, future work needs to focus on how to use the model to make predictions and give uncertainty estimates. One possible method may be to automate the optimization process to find the "best" parameter set. Our assessment of "goodness-of-fit" has been entirely by eye. A more robust approach would be to define a weighted objective function. The model runs fast, < 1 minute for a 150 year spin-up and 50 year main run on a Linux machine – and is, therefore, suited to this kind of optimization process. However, there is a vast parameter space. This parameter space could be reduced dramatically by making use of allometric relationships, *i.e.* moving further towards a pure size-based rather than a size-resolved, size- and species-based approach.

Finally, is the model flexible enough to allow for future changes? The model is flexible in some ways; diet composition, for example, is an output rather than driver. Even by constructing a more comprehensive species assemblage, the model cannot take account of future changes in the North Sea species composition, *e.g.* invading species taking advantage of climate change. The impact on the LFI of past changes in species composition could be explored using current data to see whether this possibility should be considered in modelling work.

2.4 Evaluation of reference levels for North Sea fish community indicators using a multispecies size spectrum model

2.4.1 Introduction

A key tenet of the ecosystem approach to fisheries (EAF) is to ensure that fishing effects on fisheries and the environment are sustainable. Systems based on indicators and reference points are usually used to track progress towards sustainability.

Meeting sustainability objectives for fisheries and the environment requires knowledge of the trade-offs between catches and fishing impacts. In Europe, the need for this knowledge is particularly pressing following the adoption of the Marine Strategy Framework Directive (MSFD; EC 2008a), because one of the main aims of the MSFD is to achieve Good Environmental Status (GES) for ecosystem components and attributes (*e.g.* populations, communities, foodwebs, seabed habitats, biodiversity) that are impacted by fishing. The MSFD therefore states that actions taken under the Common Fisheries Policy (CFP), the European instrument for fisheries management, should help to achieve GES. The CFP also seeks to achieve high and sustainable yield from fished stocks.

The CFP will be revised in 2012 (EC 2008b). We expect that the 2012 revision of the CFP will identify maximum sustainable yield (MSY) as the management target for fished stocks because European countries have already signed up to this target at the World Summit on Sustainable Development (WSSD). Knowledge of trade-offs between the objectives of the MFSD and CFP is needed to test the feasibility of simultaneously meeting environment and fisheries objectives, to inform the selection of reference points and to ensure that any incompatibilities and their consequences are recognized at the outset. If knowledge of these trade-offs does not inform decisions about the definitions of GES and the objectives of the CFP then there are risks that (i) all objectives could not be met simultaneously and (ii) the policies will not be regarded as workable or credible by stakeholders.

Size-based indicators are often used to describe the state of fish communities. An indicator describing the proportion of "large" fish in the community has been adopted by the Oslo and Paris Commission (OSPAR) and the EC (EC 2008b). A reference point has been proposed for this indicator in the North Sea, specifically that the proportion of the total weight of catches taken during the Quarter 1 groundfish survey and consists of fish with total length >40cm should be at least 0.3.This raises two issues. First, can the reference point be achieved if target stocks are fished at MSY and, if not, how much yield you would have to forgo to meet the proposed reference point? Second, does achieving the reference point for this indicator necessarily mean that target stocks will be at MSY (*i.e.* can the fish community reference points be met by perverse fishing strategies that would not be consistent with achieving MSY for target species)? For a second size-based indicator adopted by the EC (EC 2009), the mean maximum size of fish in the community, no reference point has been proposed. For this indicator, that provides a measure of the life-history composition, it would inform the debate on fisheries-conservation trade-offs to know how values of the indicator change in response to fishing mortality and MSY targets for component species.

Size-based models are ideal for exploring the trade-offs between fisheries and environmental management. This is because they capture the main interrelationships between population and community dynamics, as supported by theoretical and empirical analysis, and can be used to provide abundance and catch predictions for target populations as well as community properties such as size composition, mean maximum size and trophic level.

Here, we adapt and apply a size-based model of the North Sea fish community to explore trade-offs between fisheries (single-species MSY) and conservation (LFI) objectives for the North Sea and to examine how fish community state indicators respond to changes in fish pressure.

2.4.2 Methods

The model we employ is a dynamic size spectrum model that consists of 12 interacting fish species and a background resource community. Our model is developed from the equations of Andersen and Pedersen (2009) but with an explicit representation of multiple species-specific traits (Table 2.1). It is similar to the size-based multispecies model of Hall *et al.* (2006), but with food-dependent as opposed to predetermined growth. This is a feature that has not been represented before in this type of model.

Table 2.1. Multispecies size-spectrum model equations

	ENCOUNTER AND CONSUMPTION	
Prey size selection	$\phi\left(\frac{w}{w_p}\right) = \exp\left[-\left(\ln\left(\frac{\beta_i w_p}{w}\right)\right)^2 / (2\sigma_i^2)\right]$	M1
Volumetric search rate	$V(w) = \gamma w^n$	M2
Encountered food	$E_i(w) = V(w) \sum_j \theta_{ij} \int_0^\infty N_j(w_p) w_p \, dw_p$	M3
Maximum consumption rate	$I_{max} = h_i w^n$	M4
Feeding level	$f_i(w) = \frac{E_i(w)}{E_i(w) + I_{max}}.$	M5
Growth and reproduction		
Maturation function	$\psi(w) = \left[1 + \left(\frac{w}{w_i^*}\right)^{-10}\right]^{-1} \left(\frac{w}{W_i}\right)^{1-n}$	M6
Somatic growth	$g_i(w) = (\alpha f_i(w) h_i w^n - k_i w^p)(1 - \psi(w))$	M7
Gonadal growth	$g_r(w) = (\alpha f_i(w) h_i w^n - k_i w^p)\psi(w)$	M8
Recruitment		

Physiological recruitment	$R_{p.i} = \epsilon/(2w_0 N_i(w_0)g(w_0)) \int_{w_i^*}^{W_i} N_i(w)g_r(w)dw$	M9
Recruitment	$R_i = \min\left(R_{p.i}, R_{max.i}\right)$	M10
Mortality		
Background mortality	$\mu_0 = Z_0 W^z$	M11
Predation mortality	$\mu_{p.i}(w) = \sum_j \int_{w_0}^{\infty} \phi\left(\frac{w'}{w}\right)\left(1 - f_j(w')\right)V(w')\theta_{ij}N\_j(w')dw'$	M12
Resource spectrum		
Growth rate	$\frac{\partial N_r(w)}{\partial t} = r_0 w^{n-1}(\kappa(w) - N_r(w)) - \mu_{p.r}(w)N_r(w)$	M13
Carrying capacity	$\kappa(w) = \kappa_r^{-\lambda}$	M14

2.4.3 Model Overview

The model provides predictions of the *size spectrum* of each species $N_i(w)$ where w is the weight of an individual. The size spectrum can be used to find the number of individuals per volume in the size range $[w{:}w+dw]$ as $N_i(w)dw$. The size spectrum is therefore similar to a probability distribution, except that the integral of the size spectrum $\int N_i(w)dw$ is not one, but the total number of individuals, from larvae to adults. The size spectrum is found from a numerical solution of the classical McKendrick-von Foerster equation which is just a mathematical formalization of the conservation of numbers of individuals:

$$\frac{\partial N_i}{\partial t} + \frac{\partial g(w)N_i}{\partial w} = -\mu(w)\,N_i\,,$$

where $g(w)$ and $\mu(w)$ are the somatic growth and mortality of an individual with weight w. The conservation equation provides a means of scaling from individual processes (growth and mortality rates) to population structure (size distribution of each species) and community structure (sum of size distributions of all species). The conservation equation is supplemented with a boundary condition specifying how recruits join each population:

$$\frac{\partial g(w_0)N_i}{\partial w} = R_i\,,$$

where R_i is the recruitment of species i. The core of the model is therefore the descriptions of growth, mortality, and recruitment. The description of these processes largely follows those of the North Sea model of Andersen and Ursin (1977). The main processes in the model are detailed below.

Encounter and selection of food: Food is either fish from the species size spectra or from the background resource community, which is made up of planktonic and benthic organisms. Food is selected by an individual based on a preference depending on prey size and species. Selection of prey size is based on the ratio between predator and prey size and described by the classical lognormal size selection model (Ursin 1973). Consumption of encountered food is described by a type II functional response to represent satiation. The feeding level is the amount of consumed food relative to maximum consumption.

Growth: Consumed food is assimilated with efficiency α. Ingested food is first used for standard metabolism and activity leaving a fraction of the remaining energy for reproduction and the remainder for somatic growth. The fraction of assimilated food that is allocated to reproduction increases as individuals approach their size at maturity thus resulting in reduced allocation to somatic growth. At satiation (feeding level=1) the growth function gives rise to a von Bertalanffy like growth curve according to Pedersen *et al*. (2009) and Andersen *et al*. (2009).

Reproduction: Egg production is calculated from the energy routed to reproduction multiplied by a reproductive efficiency such that reproduction increases linearly with the cumulative energy allocated to reproduction by all spawning fish. Because this physiological recruitment does not always allow stable coexistence of all the species, recruitment is capped at some maximum value for each species ($R_{max\ i}$). Overall this results in a "hockey-stick" recruitment function. The rising part of the hockey stick is given by the physiological recruitment and the upper flat part is a species-specific maximum value of recruitment.

Mortality: Total mortality is composed of a constant background mortality and predation mortality; most important is the predation mortality derived to ensure that there is mass balance in the model, *i.e.* that all consumption by predators results in a corresponding mortality on its prey (Andersen and Ursin, 1977).

Resource spectrum: The smallest individuals in the model do not eat fish belonging to the fish spectra but do consume smaller planktonic or benthic organisms. For simplicity, this production is described by a background resource spectrum where each size class has semi-chemostatic growth with a fixed carrying capacity.

Solution procedure: The model is solved numerically using standard finite-difference techniques for partial differential equations. The size axis is discretized with 100 logarithmically spaced grid points and the time-step is 1 year.

2.4.4 Parameterization of the model to the North Sea fish community

To model 12 species in the North Sea, a set of specific-species parameters were obtained from available literature and datasets (Table 2.2). A remaining set of parameters fixed to be the same for all species were used and are given in Table 2.3.

Table 2.2. Species-specific parameters used in the model. Maturation weight=w^*, Asymptotic weight=W, Food intake rate=h, volumetric search rate γ (g^{-q} yr^{-1}), preferred predator prey mass ratio= β, width of prey size preference= σ. Initial values for offspring number density=$N_{i(w0)}$, calibrated maximum recruitment parameters = R_{maxi}. The mixed fishery categories are denoted as industrial=I, beam trawl= B, demersal otter trawl=T and pelagic purse-seine fishery=P. w_F = minimum size caught by the fishery, F_{base} = 1991 average fishing mortality for each species (ICES 2007) and observed yield in terms of landings (tonnes/yr) for 1991 (ICES 2007).

Species	w*	W	h	γ	β	σ	Ni(w0)	cRmaxi	Fishery	wF	Fbase	Yobs
Sprat	15.7	32.2	10.3	1.41E-11	10000	1	1.01E+15	1.15e+12	I	4	0.25	136712
Sandeel	3.6	34.5	14.5	1.33E-11	10000	1.5	1.01E+15	2.55e+12	I	5	0.764	898959
Norway pout	46.9	86.1	11.5	1.77E-11	1000	1	4.60E+14	2.50e+11	I	10	0.882	186600
Herring	111.1	203.7	11.5	1.05E-11	10000	1.5	3.21E+14	3.47e+11	P	100	0.4893	658000
Dab	21.7	211.2	7.7	8.87E-12	100	1.5	3.21E+14	1.20e+12	B	165	0.5	7155
Grey Gurnard	60.7	612.1	13.6	1.76E-11	10	1.5	7.23E+12	2.70e+10	T	115	0.7356	124975
Whiting	150.2	684.4	12.3	2.39E-11	10	1	3.41E+12	3.53e+09	T	165	0.447	33500
Sole	103.3	886	7.7	8.87E-12	100	1.5	7.23E+12	1.08e+09	B	115	0.5	4000
Plaice	203.2	3023.1	8.7	1.00E-11	100	1.5	1.93E+14	3.13e+10	B	260	0.72	229063
Haddock	334.7	3118	13.9	1.07E-11	1000	2	3.41E+14	1.81e+09	T	175	0.9	97021
Cod	3337.4	19428.6	30.9	5.34E-11	100	1	2.86E+13	1.12e+08	T	500	0.887	121204
Saithe	1459.7	45627.2	12.5	1.93E-11	1000	1	9.74E+14	2.59e+09	T	988	0.587	108000

Table 2.3. Fixed parameters.

SYMBOL	DESCRIPTION	VALUE	UNITS
α	Assimilation efficiency	0.6	-
ϵrepro	Reproductive efficiency	0.2	-
w0	Egg weight	0.001	g
n	Exponent of max. consumption	¾	-
q	Exponent of search volume	0.8	-
p	Exponent of standard metabolism	¾	-
k	Standard metabolism	0	g 1-n yr-1
Z0	Pre-factor for background mortality	0.84	yr-1
Z	Exponent of background mortality	-0.25	g 1-n yr-1
R0	Productivity of resource spectrum	10	g 1-n yr-1
κ	Carrying capacity of resource spectrum	1012	g λ-1 vol-1
λ	Exponent of resource spectrum	2+q-n = 2.05	-
wcut	Cut-off size of resource spectrum	100	g
wF	Smallest fished weight	10	g

Table 2.4. Species interaction matrix θ_{ij} based on spatial co-occurrence derived from IBTS data.

	Cod	Dab	Gurnards	Haddock	Herring	Norway pout	Plaice	Saithe	Sandeel	Sole	Sprat	Whiting
Cod	1.00	0.57	0.56	0.52	0.58	0.46	0.44	0.28	0.24	0.31	0.37	0.77
Dab	0.57	1.00	0.54	0.34	0.57	0.26	0.48	0.09	0.27	0.34	0.43	0.66
Gurnards	0.56	0.54	1.00	0.42	0.51	0.34	0.41	0.17	0.21	0.27	0.34	0.63
Haddock	0.52	0.34	0.42	1.00	0.38	0.51	0.23	0.31	0.13	0.08	0.14	0.55
Herring	0.58	0.57	0.51	0.38	1.00	0.32	0.46	0.13	0.25	0.32	0.42	0.69
Norway pout	0.46	0.26	0.34	0.51	0.32	1.00	0.16	0.31	0.08	0.06	0.09	0.46
Plaice	0.44	0.48	0.41	0.23	0.46	0.16	1.00	0.08	0.18	0.35	0.41	0.54
Saithe	0.28	0.09	0.17	0.31	0.13	0.31	0.08	1.00	0.03	0.04	0.03	0.25
Sandeel	0.24	0.27	0.21	0.13	0.25	0.08	0.18	0.03	1.00	0.14	0.18	0.28
Sole	0.31	0.34	0.27	0.08	0.32	0.06	0.35	0.04	0.14	1.00	0.32	0.36
Sprat	0.37	0.43	0.34	0.14	0.42	0.09	0.41	0.03	0.18	0.32	1.00	0.44
Whiting	0.77	0.66	0.63	0.55	0.69	0.46	0.54	0.25	0.28	0.36	0.44	1

We assumed that interactions between species were the result of spatial co-occurrence and size suitability. Assuming all species interact with each other in the model is equivalent to assuming that all species occur homogenously across the whole of the North Sea. To account for differences in spatial distribution, spatial-co-occurrence of species was calculated from IBTS catch rates that were averaged over the 1985–1995 period. Spatial co-occurrence of each pair of species was simply the number of rectangles in which both species were present divided by the total number of surveyed rectangles in the North Sea.

Preferred predator-prey size is given by a lognormal size selectivity function which takes as parameters a mean and a standard deviation. The mean and standard deviation of the preferred predator-prey size ratios were based on a published database of predators and their prey (www.cefas/dapstom, Pinnegar and Stafford 2007). Preferred prey size and diet breadth were adjusted to account for available prey abundance and size selection under 'average' conditions. These were consistent with previous values used in multispecies models (Andersen and Ursin, 1977; Lewy and Vinther, 2004).

2.4.5 Fishing mortality

Fishing mortality is added as a size-dependent component of the mortality function in the community model for each species. A knife-edge selectivity function was used to describe the ability of the fishery to catch each species. Each species had a minimum size w_F at which individuals become caught by the fishing gear and above this threshold fishing mortality F_i was assumed to be constant across all sizes. We chose a baseline year, 1991, to represent and calibrate the model. The w_{Fi} and F_i values were obtained from the estimated weight-at-age and F-at-age in 1991 given by singles-species stock assessments (ICES, 2007).

2.4.6 Model calibration and fitting procedure

To represent a baseline year of 1991, modelled yield values for each species were fit to observed yield/landings (tonnes/yr) by tuning the maximum recruitment $R_{max,i}$ (Andersen and Ursin, 1977).

All parameters in the model are determined from the physiological characteristics of each species, except the recruitment parameters and the efficiency of reproduction $\varepsilon repro$ (Table 2.3). This parameter represents density-dependent effects for each species. In the model it is used as a tuning parameter to make the model produce observed yield (catch) for each species. Formally this is performed by carrying out an unconstrained minimization of the error between observed and modelled catches and the observed and calculated B_{lim} of all twelve species at once.

2.4.7 Fishery Scenarios and Analyses

Changing the level of fishing mortality on the community was investigated for each species in isolation (representing a single-species "clean" fishery). The "clean" fishery assumes that only the targeted species is fished and all other species are unaffected by changes in fishing mortality. Although more realistic "mixed" fishery scenarios and multispecies maximum sustainable yield are currently being investigated with this model, we report results obtained from this simplified scenario for the purposes of demonstrating the general approach and for comparison of single-species MSY with the LFI.

2.4.8 Size-based Community Indicators

Four fish community indicators were calculated from the modelled community:

i) Slope of the community size spectrum. This was calculated as the slope obtained from a linear regression the log (total abundance of individuals) vs. log (body mass).

ii) Mean weight of all individuals in the community.

iii) Mean maximum weight was calculated as: $\overline{W_{\max}} = \sum_i (W_{\max i} B_i) \Big/ B$

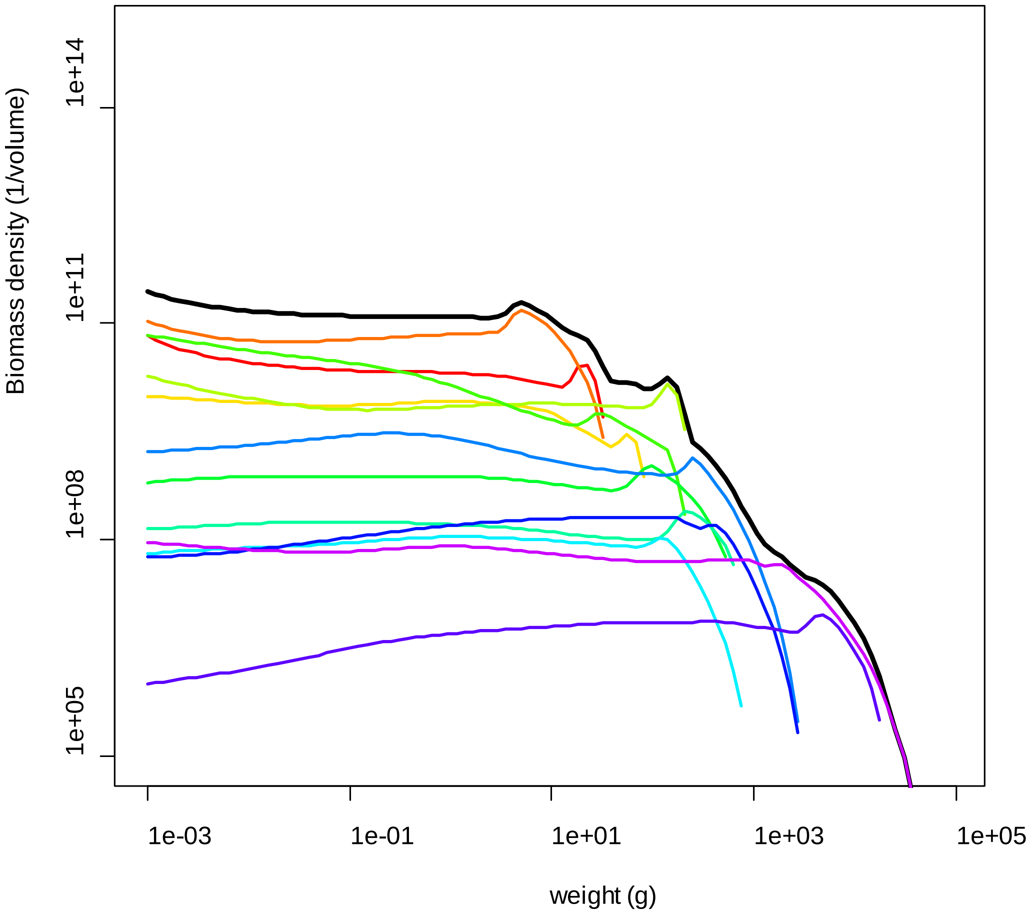
where $W_{\max i}$ is the maximum weight of species i, B_i is the biomass of individuals of species i and B is the total biomass of all individuals. Asymptotic weight (W_∞) was used as a measure of maximum weight.

iv) The proportion of "large fish", LFI, was calculated as: $P_{>40cm} = \dfrac{W_{>40cm}}{W_{Total}}$

where $W_{>40cm}$ is the weight of fish greater than 40 cm in length and W_{Total} is the total weight of all fish in the sample. Only sizes > 10 grammes were used in the calculation of the above indicators for consistency with empirically-based indicators. Indicators were calculated based on "demersal species" only (*i.e.* sprat, herring and sandeel were excluded).

2.4.9 Results

The time-averaged modelled size spectra for each species are shown in Figure 2.9. The model produced a dynamic equilibrium driven by feedback between predators and prey that arise from the growth process. Our preliminary calibrated model resulted in yields that are within +/- 50% of observed catches and modelled growth rates were also consistent with observed mean weight-at-age for each species.


Biomass density (1/volume)
1e+14
1e+11
1e+08
1e+05
1e-03
1e-01
1e+01
1e+03
1e+05
weight (g)

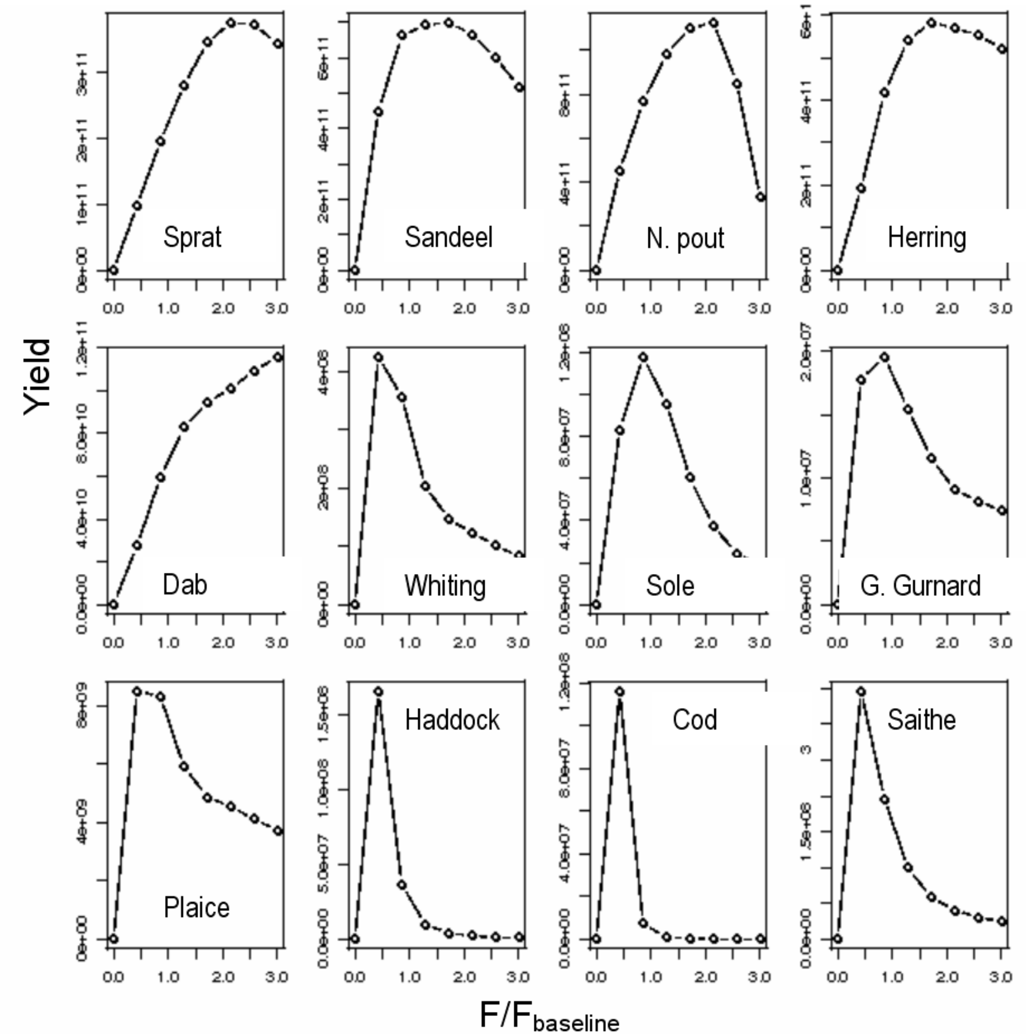
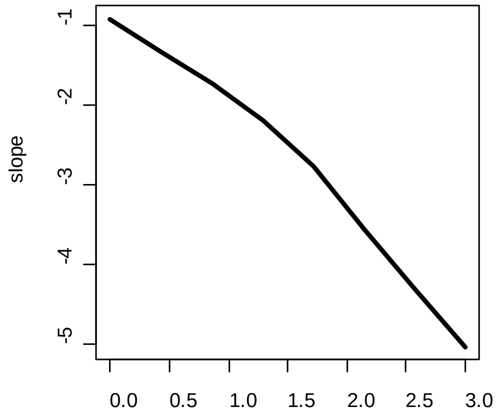


Figure 2.10. Modelled yield in terms of weight (grammes/yr) at increasing levels of fishing mortality relative to the $F_{baseline}$.

To investigate how the community indicators responded to changes in fishing pressure, we focus on the single-species "Cod" fishery scenario. All of the indicators declined monotonically with increasing F_{Cod} (Figure 2.11) and reductions resulted in recovery of the indicators. The LFI indicator was approximately 0.15 under the baseline conditions and halving the F_{Cod} resulted in an LFI value of 0.3. Our preliminary model results also show that halving the $F_{baseline}$ would also be needed to achieve the F_{MSY} for Cod (Figure 2.10).


slope
-1
-2
-3
-4
-5
0.0
0.5
1.0
1.5
2.0
2.5
3.0

ever, there are several problems with the notion of a single-species MSY that need to be considered when making multispecies extensions. First, MSY assumes that no other species yields are affected either directly or indirectly by the fishery but in reality fisheries are mixed. Second, it also does not provide for the indirect effects of fishing one species on the yield of other species (via the trophic interactions). The multispecies maximum sustainable yield (MMSY) which seeks to achieve maximum yield of all species in terms of catch also has some problems when several mixed fisheries are taken into account (Collie *et al*. 2003). Because the objective of each fishery is to maximize economic yield, the MMSY will not be directly proportional to MMEY (Multispecies Maximum Economic Yield) because the economic value of the species caught by each fishery differs substantially. We are currently incorporating these aspects into our modelling work. Furthermore, this model is being used in a management strategy evaluation framework to investigate reference levels of community indicators and evaluate the performance and responsiveness of indicators (particularly LFI) to management. This is in conjunction with a virtual-survey model to evaluate the bias and uncertainty in calculated indicators that can arise from sampling programmes and also to provide a means of comparing the empirically derived LFI to a modelled LFI that takes into account the effects of gear selectivity and observation error.

2.5 Data fitting and uncertainty

Both models presented here have been fit to North Sea fish community data. These models represent the first attempt to fit size-structured, multispecies models to real fish assemblages; previous work has modelled a generic system loosely based on a real-world fish community (*e.g.* Hall *et al*. 2006). This exercise has highlighted some of the limiting factors in and implications for fitting these models to data.

A reasonable fit to multiple datasets can be achieved with these models. A robust definition of "reasonable fit" is required. For FishSUMS, model fitting was been entirely by eye: the parameter values of the models have been tuned until the model output appeared to closely match the available data on landings, stock biomass, etc.

A robust and efficient approach is to define a function, such as a weighted difference between the model output and data, to be minimized as a function of model parameters. This process can be automated, although in practice this depends on the speed of model code and size of parameter space.

The size spectrum model (Chapter 4) successfully used unconstrained minimization of the difference between observed and modelled landings (implemented in R), as a function of unknown parameters, to fit the model.

There is a huge amount of data available but also many gaps, *e.g.* both models experienced difficulties with obtaining grey gurnard and common dab fishing mortalities. Work that looks at estimating life-history parameters and data such as fishing mortality and recruitment is critical to the future development of multispecies models; model development should inform future data collection.

Data availability may still prevent us from building fish community models suitable for management decision-making: "while computing power and measurement techniques both advanced greatly in the past 10 years, the limiting factor in developing multispecies models and applying them to management is still the lack of sufficient information" (Rose and Sable 2009).

In lieu of further data collection, and bearing in mind that the data will never be perfectly accurate, models should perform parameter sensitivity analysis.

A proper account of uncertainty (unknown parameters, unmodelled processes and model structure uncertainty) will lead to large error bounds on any predictions. This should be acknowledged by modellers and management.

Further uncertainty comes from unmodelled and unknown processes. For example, neither model presented here takes account of environmental variability. Some processes might be better characterized as stochastic processes in order to provide error bounds on predictions.

Further uncertainty comes from lack of knowledge of what model structure is most appropriate. It is possible that "wrong" model formulations can still be fit to data (Yodzis, 1998). However, a good fit to multiple different and preferably independent datasets, as has been achieved with FishSUMS and the size spectra model, lends confidence. Future work should look at comparing predictions from a number of different models, with different underlying assumptions, in order to make ensemble predictions.

Assuming that the "best fit" parameters tell us something about the "true" parameters, fitting to data gives insight into parameters and processes. For example, it was found that multispecies predation interactions were required in order to get a good fit to North Sea fish community data; this implies the constant background mortality assumption of single-species management is flawed. It also shows where the model is lacking; for example, the FishSUMS model cannot in its current form model capture the huge variability of haddock recruitment because the processes causing this are not represented in the model.

Scenario testing can be performed using these models. For example, the size spectrum model was used to explore the impacts of fishing on multispecies maximum sustainable yield.

2.6 Recommendations

We recommend that the multispecies size-structure be applied to other systems under a wider range of scenarios. Spatial process, comparisons across ecosystems and/or spatially distinct areas within ecosystems are required for the future development of reference levels for size-based fish community metrics, as these will be different according to the productivity levels and background environmental variability.

Future work on uncertainty could include the implementation of observation and process error into the modelling frameworks and further development of formalized model-fitting procedures and sensitivity analyses. Because many of these issues are being studied by WGSAM, we recommend uptake of the models developed for evaluating size-based indicators in the North Sea be considered by that working group and encourage cross-comparison and evaluation of the different models being applied.

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3 Metrics for characterizing changes in structure, function and productivity of fish communities

ToR b) Evaluate metrics to characterize, monitor and detect changes in the structure, function and productivity of fish communities

3.1 Introduction

Current ecosystem management objectives for the North Sea demersal fish community focus on restoring its size structure. When asked by OSPAR to recommend a metric that would best support an Ecological Quality Objectives (EcoQO) for the North Sea fish community, application of the ICES criteria for a good state indicator (ICES 2001a) suggested that size-based metrics would likely perform best (ICES, 2001b; Greenstreet, 2008). The theoretical relationship between fishing mortality and fish population age composition (and hence, size structure) had long been established (Beverton and Holt, 1957), providing a strong theoretical basis for expecting increased fishing mortality (“pressure”) to reduce large fish abundance and so alter fish community size composition, and this has been born out in numerous studies (Rice and Gislason 1996; Gislason and Rice 1998; Bianchi *et al.*, 2000; Daan *et al.*, 2005; Shin *et al.*, 2005). Consequently, “Changes in the proportion of large fish and hence the average weight and average maximum length of the fish community” emerged as the Element of Ecological Quality for the “Fish Community” EcoQI at the Bergen 2002 North Sea Ministerial Conference (Heslenfeld and Enserink 2008). Subsequent work has focused on developing the most effective size based metric and setting the EcoQO (Greenstreet *et al.*, In review).

Prior to the Bergen Ministerial Declaration in 2002, however, the Convention on Biological Diversity and Annex V (Protection and Conservation of the Ecosystems and Biological Diversity of the Maritime Area) of the OSPAR convention on the “Protection of the Marine Environment of the North-East Atlantic” both focused on the sustainable use of marine natural resources to conserve biological diversity (Barange 2003). More recently, the European Union’s Marine Strategy Framework Directive (MSFD) emphasized the need to halt biodiversity loss and ultimately to provide biologically diverse and dynamic oceans and seas (Greenstreet 2008). This emphasis on biodiversity prompted many early studies of marine fish communities to examine trends in fish species diversity and relate changes to increased fishing activity (Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999; Rogers *et al.*, 1999a; Rogers *et al.*, 1999b; Rogers and Ellis, 2000; Greenstreet and Rogers, 2006). Given this political emphasis on conserving and restoring marine biodiversity, the question as to whether management measures aimed at restoring fish community size composition will also be sufficient to conserve and restore fish biodiversity needs to be examined.

This raises the question, to what extent are the size composition and species diversity of the fish community correlated? A strong mechanistic correlation would suggest “redundancy” among size-based and species diversity metrics; achieving the fish community EcoQO and restoring fish size structure should then simultaneously serve to conserve and restore fish biodiversity. However, it has generally been assumed that different aspects of the composition, structure and functioning of natural communities vary independently (Fulton *et al.*, 2005; Piet and Jennings, 2005; Greenstreet and Rogers, 2006) implying that redundancy between different univariate community metrics is in fact relatively low. If so, then a broad suite of metrics will be needed to cover all the different types of change that could occur in a community.

Consequently, establishing appropriate monitoring programmes and introducing an adequate advisory framework could have significant resource implications. A priority for the future development of an ecosystem approach to marine management (EAMM) is therefore to determine the level of covariation among the various potential "state" and "surveillance" indicators that could be applied to monitor change in different aspects of fish communities and identify the minimum number of indicators necessary to cover all attributes of the community that are of concern.

Fifteen univariate community metrics were applied to ICES International Bottom Trawl Survey (IBTS) demersal fish species abundance and abundance at length data collected between 1983 and 2008. Trends in the metrics are reported at the whole North Sea "regional" scale, repeating the process used to determine the Large Fish Indicator (LFI), which is the basis for the North Sea demersal fish community EcoQO. The LFI was one of the 15 metrics used. Initially the 15 metrics were selected to cover five broad attributes of the composition, structure and function of the demersal fish community of the North Sea: (i) abundance/biomass/productivity; (ii) size composition; (iii) species richness; (iv) species evenness; and (v) life-history trait composition. A principal components analysis (PCA) was carried out to determine the level of redundancy among the 15 metrics and identify the minimum suite of metrics that would enable all five attributes to be monitored. The value of the LFI as a potential headline surveillance metric to monitor the "health" of the demersal fish community is discussed.

3.2 Methods

ICES (2007c) advised that the fish community EcoQO should be based on the LFI using data collected by the IBTS, undertaken in the first quarter of the year (Q1). This survey, coordinated through ICES, aims to obtain two half-hour trawl samples from each ICES rectangle (0.5° latitude by 1.0° longitude) in each year and has almost complete coverage of the North Sea (ICES area IV). Since 1983, all the vessels involved have used the same Grande Ouverture Verticale (GOV) demersal trawl, providing the longest time-series of consistent sampling in the North Sea. Because of this dependency of the fish community EcoQO on the Q1 IBTS, all the analyses undertaken here used the same dataset. The GOV trawl is more selective for bottom-dwelling species. Pelagic species tend to occupy higher regions of the water column and their tendency to form schools means that more samples are required to estimate variation in abundance with the same precision as demersal species (Ehrich and Stransky 1999). Most studies that have derived univariate community metrics from North Sea groundfish survey data have therefore excluded pelagic species from their analyses (Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999; Piet and Jennings, 2005; Greenstreet and Rogers, 2006). Development of the North Sea "fish community" EcoQO has followed the same logic and only considers demersal fish (ICES, 2006). The same approach has been adopted here.

Despite a clearly stated sampling protocol, irregularities in the IBTS database are common (Daan 2001). These include provision of species counts without length frequency data, and the occasional absence of identification to species level, e.g. 'gurnards' rather than grey, red or tub gurnard. This lack of detailed information affects size-based, productivity, life-history and diversity metrics. Size-based metrics require length frequency summaries. They are also affected by the lack of specific taxonomic information if weight-at-length relationships need to be applied. Productivity metrics depend on both identification to species and the provision of appropriate length frequency data. Species diversity and life-history trait metrics can only be applied to survey data recorded to a consistent level of taxonomic resolution, preferably to species. Similarly, life-history metrics require species identification to apply the appropriate parameter appellation to the abundance data. Simply excluding incomplete records would have caused significant loss of data and compromised time-series analyses because older samples tended to be less complete. Short-cuts in data recording were also more likely when larger-than-normal trawl samples (exceptionally large catches of herring for example) were taken on board, so just discarding imperfect sample data could have introduced a systematic bias in any ensuing analyses.

Unbiased estimators for missing data were therefore derived and applied. Where species count data only were provided, a length–frequency distribution equal to that observed for the same species in the same year and region was assumed. Similarly, abundance at length data of fish identified only to genus, family or order were assumed to have a species composition equal to the relative abundance of the constituent species sampled in the same survey and year. When filling in missing species composition information in this way, variation in length was taken into account in estimating appropriate species relative abundances. For example, in the case of unidentified weever fish (Trachinidae), all fish > 15 cm were assumed to be greater weever *Trachinus draco*. Below this length unidentified weever fish were assigned to *T. draco* or lesser weever *Echiichthys vipera* depending on their relative abundance within defined length classes, e.g. 12 cm to 15 cm, < 12 cm, etc. Species abundance at length data were checked to eliminate records of impossibly large individuals. All records where the species length exceeded the maximum length for the species (L_{max}) recorded in *FishBase* (http://www.fishbase.org/search.php) were examined. Extreme outliers were either deleted, or the length was changed to the L_{max} for the species, if this length appeared to fit in the general length frequency distribution observed in the rest of the data. If the length recorded was only marginally greater than L_{max} in *FishBase* (e.g. no more than 5% greater), and it fit in the general length frequency distribution, then no action was taken. In total, these corrections affected less than 0.2% of the 904,000 records in the database.

Although haul duration tended to be standardized to half-hour tows (except Scotland continued to fish for 1 hour until 1999), some variation occurred due to variable operational circumstances. Tow speeds also varied due to changing weather conditions and differences between vessels. To standardize the data, all catch abundances at length were converted to densities at length per km^2 of area swept between the wings of the trawl. For some samples the distance trawled could not be determined. In such cases the mean trawl speed for the vessel concerned, and for the year in question, was applied so that trawl distance could be estimated from tow duration. On occasions where the necessary wing spread data were missing, this was estimated using a relationship between wing spread and water depth determined following the same procedure used by Fraser *et al.* (2007). Fifteen univariate community metrics were calculated using the Q1 IBTS demersal species density and density at length data (Table 3.1). All the survey data collected in each year were aggregated to determine average density at length for each species across the entire North Sea. Annual values for each metric were then computed and temporal trends established.

Table 3.1. Descriptions, abbreviations and derivations of the fifteen univariate community metrics applied to the groundfish survey data. Metrics 1 to 4 are metrics of abundance/biomass/productivity. Metrics 5 and 6 are metrics of size composition. Metrics 7 and 8 are metrics of species richness. Metrics 9 to 11 are metrics of species evenness. Metrics 12 to 15 are life-history trait composition metrics.

Number	Metric	Abbreviation	Metric calculation	Terminology
1	Biomass	B	$B=\sum_{s=1}^{S}\sum_{l=\min}^{l=\max}\sum_{n_{s,l}=1}^{N_{s,l}} c_s l^{b_s}$	Where S is the total number of species, *l* is the length class, $N_{s,l}$ is the total number of individuals in each length class of each species. The constants c_s and b_s are the constant and exponent values respectively in the species-specific weight at length relationship.
2	Abundance	N	$N=\sum_{s=1}^{S}\sum_{l=\min}^{l=\max} n_{s,l}$	Where *S* is the total number of species, *l* is the length class, and $n_{s,l}$ is the number of fish in each species and length class.
3	Overall daily growth production	P	$P=\sum_{s=1}^{S}\sum_{l=\min}^{l=\max}\sum_{n_{s,l}=1}^{N_{s,l}} c_s b_s l^{b_s-1}\frac{k_s}{365}\left[l_{\infty,s}-l\right]$	Where S is the total number of species, *l* is the length class, $N_{s,l}$ is the total number of individuals in each length class of each species. The constants c_s and b_s are the species-specific weight at length relationship constant and exponent values respectively. The constants k_s and $l_{\infty,s}$ are the species-specific von Bertalanffy growth function growth and ultimate body length values respectively. k_s is divided by 365 to convert the annual parameter to a daily parameter.
4	Specific daily growth production	P/B	$"P/B"=\frac{P}{B}$	Where *P* is the total daily growth production and *B* total biomass of the fish community (see above).
5	Large fish indicator	LFI	$"LFI"=\frac{\sum_{s=1}^{S}\sum_{l>40cm}^{l=\max}\sum_{n_{s,l}=1}^{N_{s,l}} c_s l^{b_s}}{B}$	For term explanations, see “Biomass” above. Note that in the numerator, the summation is carried out across lengths >40cm only.
6	Mean weight of fish	W	$W={}^{B}\!/_{N}$	Where *B* is the total biomass and *N* the total number of fish in the sample (see above).
7	Species count	S	S	Where *S* is the count of the number of species in the sample.
8	Margalef’s species richness	SMarg	$S_{M\arg}=\frac{(S-1)}{LogN}$	Where *S* is the total number of species and *N* the total number of individuals in the sample (see above)

NUMBER	METRIC	ABBREVIATION	METRIC CALCULATION	TERMINOLOGY
9	Pielou's evenness	J	$J = \dfrac{-\sum_{s=1}^{S} N_s/N \log N_s/N}{LogS}$	Where N_s is the number of individuals belonging to species s, N is the total number of individuals of all species in the sample, and where S is the total number of species recorded in the sample (see above).
10	Hill's N1 diversity	N1	$"N1" = e^{-\sum_{s=1}^{S} \frac{N_s}{N} \log \frac{N_s}{N}}$	Where N_s is the number of individuals belonging to species s, N is the total number of individuals of all species in the sample, and where S is the total number of species recorded in the sample (see above).
11	Hill's N2 dominance	N2	$"N2" = 1 \Big/ \sum_{s=1}^{S} \frac{N_s}{N}$	Where N_s is the number of individuals belonging to species s, N is the total number of individuals of all species in the sample, and where S is the total number of species recorded in the sample (see above).
12	Mean ultimate body length	L∞	$L_{\infty} = \dfrac{\sum_{s=1}^{S} \sum_{n_s=1}^{N_s} l_{\infty,s}}{N}$	Where $l_{\infty,s}$ is the von Bertalanffy ultimate body length of each species s. S is the total number of species recorded in the sample and N_s is the total number of individuals of each species caught. N is the total number of individuals recorded in the sample.
13	Mean growth coefficient	K	$K = \dfrac{\sum_{s=1}^{S} \sum_{n_s=1}^{N_s} k_s}{N}$	Where $k_{,s}$ is the von Bertalanffy growth parameter for each species s. S is the total number of species recorded in the sample and N_s is the total number of individuals of each species caught. N is the total number of individuals recorded in the sample.
14	Mean length at maturity	Lmat	$L_{mat} = \dfrac{\sum_{s=1}^{S} \sum_{n_s=1}^{N_s} l_{mat,s}}{N}$	Where $l_{mat,s}$ is the length at maturity of each species s. S is the total number of species recorded in the sample and N_s is the total number of individuals of each species caught. N is the total number of individuals recorded in the sample.
15	Mean age at maturity	Amat	$A_{mat} = \dfrac{\sum_{s=1}^{S} \sum_{n_s=1}^{N_s} a_{mat,s}}{N}$	Where $a_{mat,s}$ is the age at maturity of each species s. S is the total number of species recorded in the sample and N_s is the total number of individuals of each species caught. N is the total number of individuals recorded in the sample.

Principal components analysis (PCA; SYSTAT©) was applied to the temporal trend data to determine the level of covariation among the 15 metrics and to identify key metrics that would allow surveillance of all major aspects of the composition, structure and functioning of the demersal fish community in the North Sea. Generally, three or four principal components explain most of the variance in the majority of PCAs. However, because the fifteen metrics were deemed to measure five separate attributes of the fish community's composition, structure and functioning, the PCA was initially forced to derive six principal components, thereby building into the analysis the potential to identify further previously unconsidered attributes. A model minimizing procedure was then employed to reduce the number of principal components and identify the essential metric groupings. The product of the component loadings for each metric and the percentage of variance explained by each of the components were determined. This product was then used to reassign metrics to alternative components, so that each metric was assigned to the component where this product, rather than the initial loading, was highest. If this process resulted in a component no longer having metrics any associated with it, the PCA was repeated and forced to derive one fewer principal components. This process was repeated until no further principal components could be eliminated.

3.3 Results

To illustrate any general underlying trends, polynomial (4th degree) smoothers were fitted to the North Sea scale temporal trend data for each of the 15 metrics (Figure 3.1). Clear differences were apparent between trends, suggesting that the different attributes of the demersal fish community were responding in different ways. The minimizing procedure reduced the initial six down to four principal components, but only reduced the proportion of total variance explained from 98% by six components, through 96% by five components, to 91% by four components (Table 3.2). Fourth degree polynomial smoothers fitted to the principal component scores suggested clear underlying temporal trends in the first three principal components. Conversely, the fourth principal component was poorly fitted by the smoother; this last principal component effectively captured the residual variation unexplained by the drivers underlying the trends shown by the first three principal components, and may therefore have been more responsive to a shorter term, i.e. interannual, or every two or three years driver (Figure 3.2).

For nine metrics, trends in the scores of their linked principal component explained over 70% of variation in the actual metric values. For a further five, the principal component scores explained 50% to 70% of variance. Only for one metric (P/B) was less than 50% of variation in the original data explained by the principal component scores trend (Table 3.3). For all but one of the metrics, the P/B ratio being the exception, the polynomial smoothers fitted to the principal component score trends also explained a significant proportion of variation in the original metric values associated with each factor (Table 3.3). Indeed, the smoother fitted to the second principal component scores actually explained more of the variation in the original LFI than did the actual component scores. The smoother fitted to the third principal component scores explained almost the same amount of variation in both original species richness metric trends as the actual component scores. The smoother fitted to the first principal component scores explained between 77% and 82% of the variation in the two Hill's species evenness metrics explained by the component scores (Table 3.4). Thus, for the three principal components where 4th degree polynomial smoothers fitted trends in the principal components scores reasonably well, these smoothers explained almost as much, if not the same amount, of variation in the actual metric values as the principal component scores did themselves. Assuming that the polynomial smoothers provide an indication of the actual response to some underlying driver, this analysis could be used as a diagnostic tool to select particular metrics for inclusion in any suite of surveillance metrics.

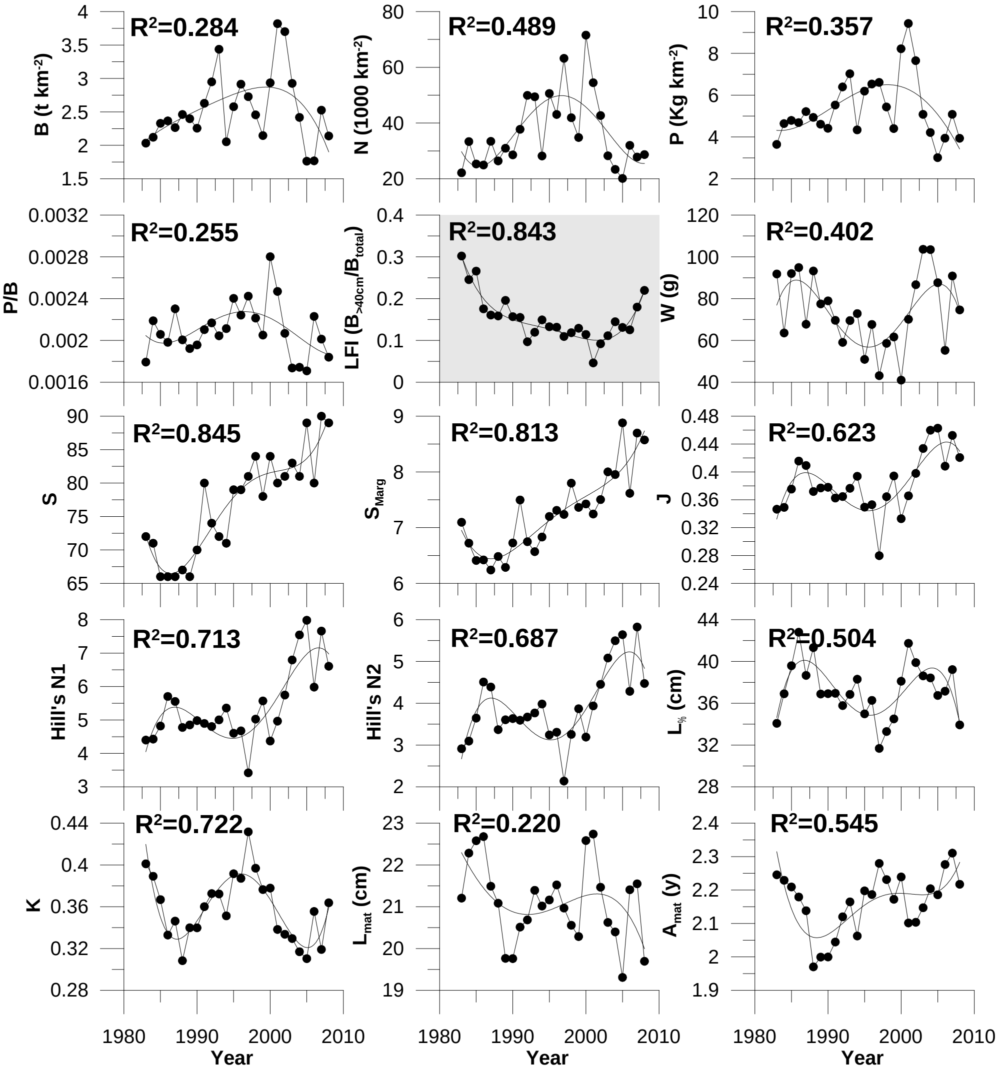

Figure 3.1. Trends in fifteen indicator metrics applied to the IBTS Q1 groundfish survey data for the whole North Sea. See Table 3.1 for explanation of metrics (y-axis labels). The proportion of large fish indicator on which the North Sea fish community EcoQO is based is highlighted. Fitted smoothers are 4th degree polynomials and R2 values indicate goodness-of-fit.

Table 3.2. Summary of results of principal components analysis for whole North Sea. Brackets indicate a negative correlation between factors and variable. The percentage of the total variance explained by each principle component, along with the total variance explained, is given. Shaded cells show the consequences of the factor minimizing process; metrics that were reassigned from their original principle component (light grey fill) are also shown linked with the principle component to which they were reassigned (darker grey fill).

Principle Component	PC1	PC2	PC3	PC4	PC5	PC6	Total
Variance explained	30.5	19.2	15.2	13.1	11.2	9.0	98.1
Metrics linked to Each principle component. First analysis with six factors.	(J)	B	S	(P/B)	Lmat	Amat	
	(N1)	P	SMarg	W	L∞		
	(N2)	(LFI)					
	K	N					
	N						
	P/B						
	(W)						
	(L∞)						
Principle Component	PC1	PC2	PC3	PC4	PC5		Total
Variance explained	31.1	20.2	19.6	13.2	11.9		96.1
Metrics linked to Each principle component. Second analysis with five factors.	(J)	(B)	S	(P/B)	Lmat		
	(N1)	(P)	SMarg	W			
	(N2)	LFI	Amat				
	(L∞)	(N)					
	K						
	N						
	P/B						
	(W)						
Principle Component	PC1	PC2	PC3	PC4			Total
Variance explained	35.1	23.5	20.3	12.4			91.4
Metrics linked to Each principle component. Third analysis with four factors.	J	B	S	Lmat			
	N1	P	SMarg				
	N2	(LFI)	Amat				
	L∞	N					
	(K)						
	(P/B)						
	W						
	(N)						

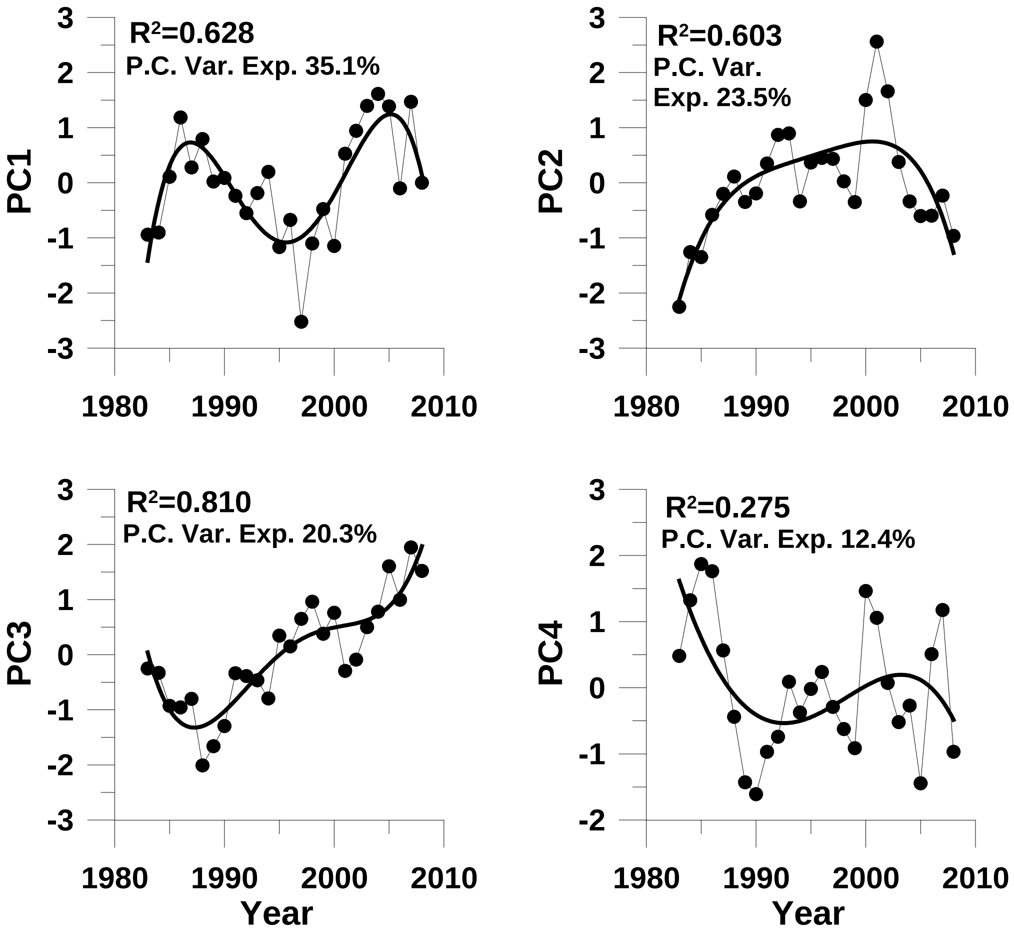

Figure 3.2. Trends in scores for each of the four final principle components fitted to 4th degree polynomial smoother to define underlying trends. R2 value indicates the goodness-of-fit of the 4th degree polynomial smoother to the actual principle component score data. P.C. Var. Exp. Indicates the percentage of total variation explained by each principle component (see Table 3.2).

Table 3.3. Correlations (R2) between individual metric values and the each of the four principle components scores and fitted 4th degree polynomial smoothers. Grey filled cells indicate the principle component to which each metric has been linked by the PCA.

		PC1		PC2		PC3		PC4	
CORRELATION	METRIC	R2	P<	R2	P<	R2	P<	R2	P<
Principle component scores	B	0.000		0.735	0.0001	-0.011		0.031	
	N	-0.391	0.001	0.533	0.0001	0.013		0.026	
	P	-0.064		0.790	0.0001	-0.004		0.099	
	P/B	-0.357	0.01	0.298	0.01	0.000		0.176	0.05
	LFI	-0.003		-0.755	0.0001	-0.033		0.046	
	W	0.668	0.0001	-0.102		-0.027		0.000	
	S	0.003		0.063		0.843	0.0001	-0.030	
	SMarg	0.068		0.000		0.810	0.0001	-0.049	
	J	0.785	0.0001	-0.042		0.096		-0.014	
	N1	0.652	0.0001	-0.023		0.281	0.01	-0.024	
	N2	0.785	0.0001	-0.002		0.162	0.05	-0.002	
	L∞	0.521	0.0001	0.066		-0.150		0.219	0.05
	K	-0.895	0.0001	-0.008		0.013		0.013	
	AMat	-0.067		-0.064		0.573	0.0001	0.237	0.05
	LMat	-0.008		0.051		-0.031		0.896	0.0001
Principle component smoother	B	-0.017		0.251	0.01	0.000		-0.051	
	N	-0.193	0.05	0.284	0.01	0.006		-0.114	
	P	-0.062		0.274	0.01	0.000		-0.056	
	P/B	-0.127		0.122		-0.004		-0.035	
	LFI	-0.013		-0.819	0.0001	-0.041		0.359	0.01
	W	0.260	0.01	-0.100		-0.004		0.123	
	S	0.026		0.082		0.799	0.0001	-0.064	
	SMarg	0.098		0.013		0.778	0.0001	-0.017	
	J	0.572	0.0001	-0.005		0.103		0.000	
	N1	0.536	0.0001	0.000		0.269	0.01	-0.003	
	N2	0.605	0.0001	0.001		0.158	0.05	-0.004	
	L∞	0.324	0.01	0.000		-0.085		0.025	
	K	-0.683	0.0001	-0.005		0.000		0.007	
	AMat	-0.005		-0.063		0.366	0.01	0.099	
	LMat	-0.010		-0.022		-0.031		0.167	0.05

Table 3.4. Ratios of the variances explained in the original metric data by the smoothers fitted to the linked principle component scores and the principle component scores themselves. Table is ordered by ranked ratio scores.

METRIC	PC	RATIO
LFI	2	1.085
SMarg	3	0.960
S	3	0.947
N1	1	0.822
N2	1	0.770
K	1	0.764
J	1	0.730
AMat	3	0.638
$L\infty$	1	0.623
N	2	0.533
W	1	0.389
P/B	1	0.358
P	2	0.347
B	2	0.341
LMat	4	0.187

The 15 metrics examined were initially selected to portray variation in five main attributes of the composition, structure and functioning of the demersal fish community. The PCA results suggested that several of these attributes do indeed vary independently of each other. For example, the two species richness metrics correlated closely (Figure 3.3A), and associated with principal component 3 (Table 3.2), whereas all three species evenness metrics also co-varied closely (Figure 3.3B), but were linked to principal component 1 (Table 3.2). Species richness and evenness of the North Sea demersal fish community must therefore vary relatively independently of each other (Figure 3.3C). A suite of surveillance indicators for the North Sea demersal fish community would therefore need to include metrics of both species richness and species evenness, but the extent of covariation suggests that only one metric would be needed to cover each attribute, reducing the number of biodiversity metrics from the five used here to just two.

Similarly, the biomass, abundance and overall productivity metrics all co-varied closely (Figure 3.4A), but this time linked to the second principal component (Table 3.2). This suggests that only one of these metrics would be necessary to perform a surveillance indicator role for this main attribute of the composition, structure and functioning of the demersal fish community. It also implies that variation in demersal fish abundance/biomass/productivity was relatively independent of variation in both species richness (Figure 3.4B) and species evenness (Figure 3.4C), although to some extent, species evenness varied inversely with abundance (Figure 3.4C).

Although the PCA linked P/B most strongly to the first principal component (Table 3.2), and indeed P/B correlated with all three species evenness metrics (Figure 3.5A), this metric was also correlated with the second principal component scores (Table 3.3). This arose through the relatively strong correlations between abundance and P/B and between overall productivity and P/B. However, the relationship between biomass and specific productivity was much weaker (Figure 3.5B). The two size composition metrics (LFI and mean weight) were not closely correlated (Figure 3.5C), and were split by the PCA between two different principal components (Table 3.2). The LFI was linked to the second principal component and was negatively correlated with the abundance, biomass and overall productivity metrics (Figure 3.5D). Mean fish weight was linked to the first principal component; it correlated negatively with specific productivity. Mean fish weight was weakly but positively correlated with the three species evenness metrics (Figure 3.5E).

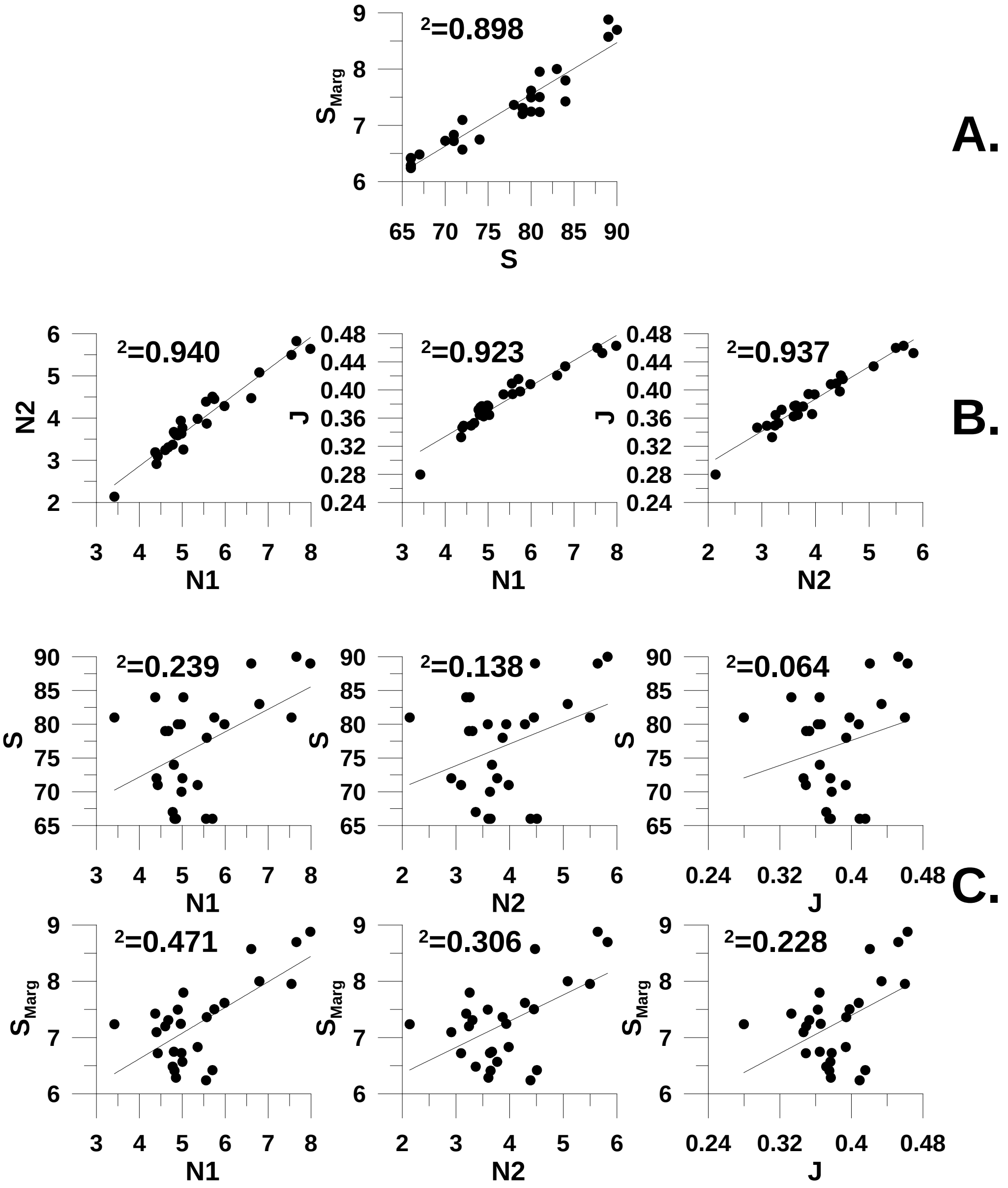

Figure 3.3. Relationships between: the two species richness metrics (A); the three species evenness metrics (B); and each species richness and species evenness metric combination (C).

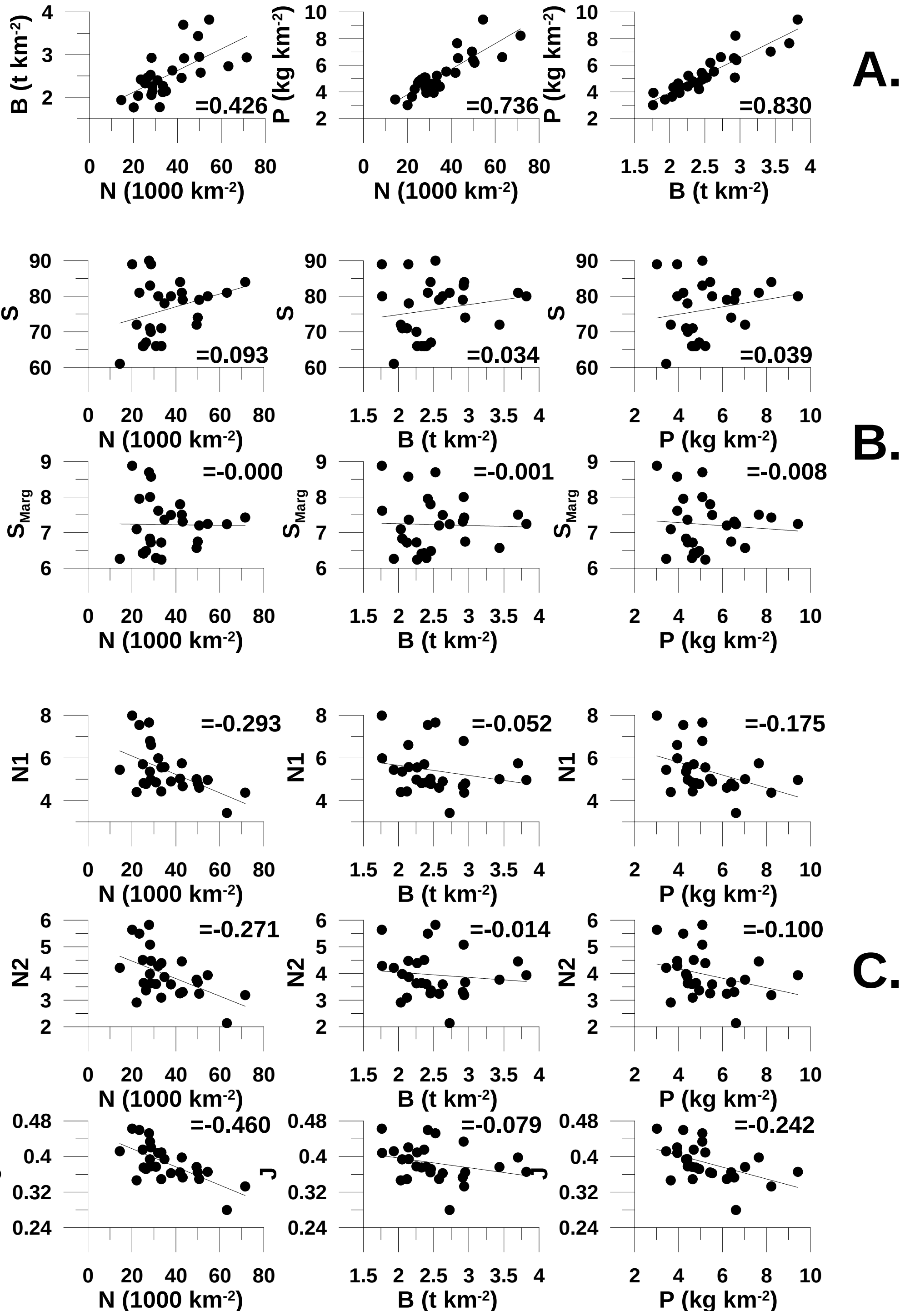

Figure 3.4. Relationships between: three abundance/biomass/productivity attribute metrics linked to PCA factor 2 (A); the three factor 2 abundance/biomass/productivity attribute metrics and the two factor 3 species richness attribute metrics (B); and the three factor 2 abundance/biomass/productivity attribute metrics and the three factor 1 species evenness attribute metrics (C).

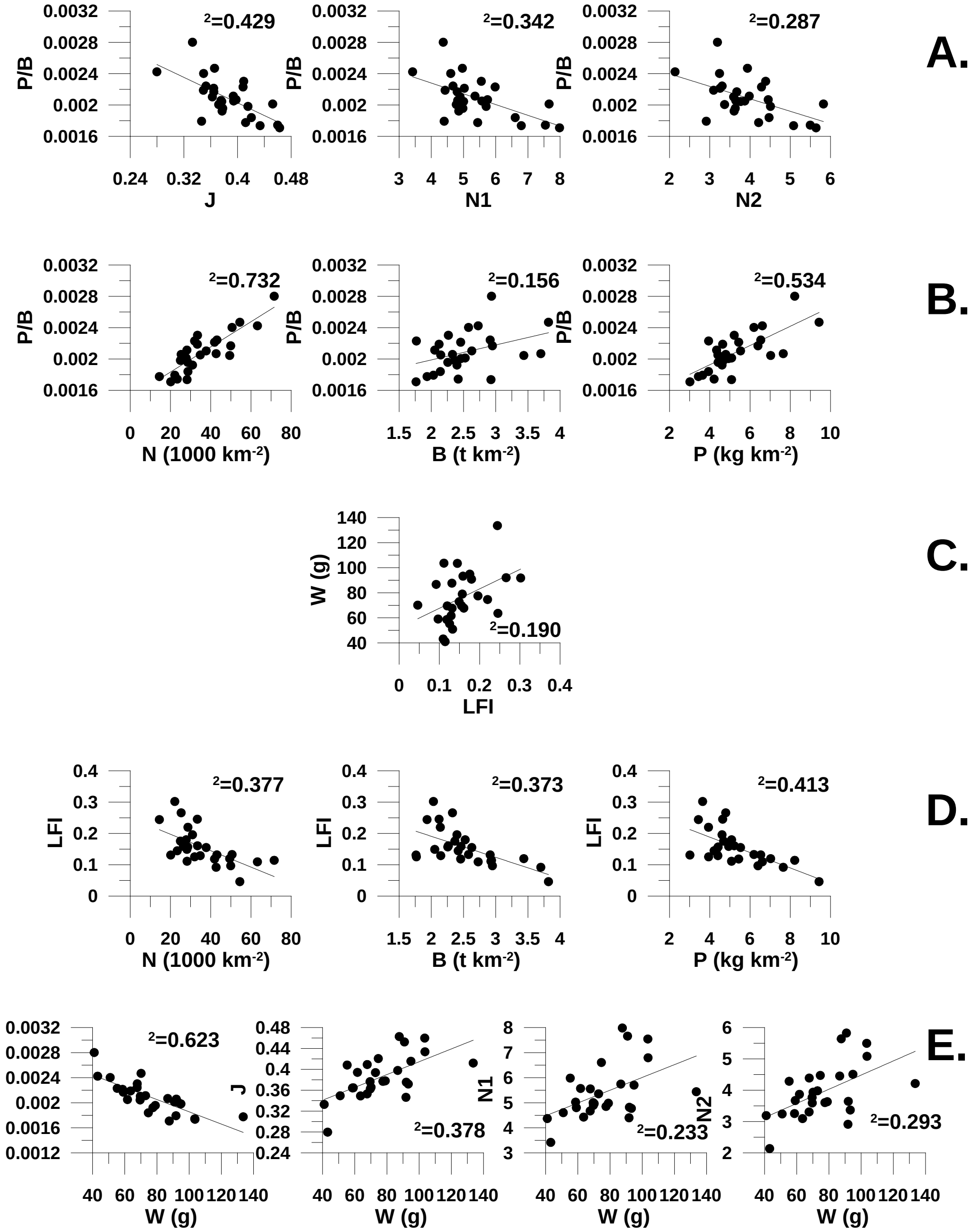

Figure 3.5. Relationships between: specific productivity and the three species evenness metrics linked together with PC1 (A); specific productivity and the three abundance/biomass/productivity attribute metrics (B); the two size composition metrics, split by the PCA between PC1 and PC2 (C); the proportion of large fish indicator and the three abundance/biomass/productivity attribute metrics, linked together to PC2 (D); mean fish weight metrics and the specific productivity and three species evenness metrics linked together with PC1 (E).

The four life-history trait metrics were distributed between three of the four principal components (Table 3.2). Ultimate body length (L_∞) and the von Bertalanffy growth parameter (K) both linked with the first principal component (Table 3.2) and, as would be expected, were correlated negatively with each other (Figure 3.6A). The von Bertalanffy growth parameter was strongly negatively correlated, while ultimate body length was only weakly positively correlated, with all three species evenness metrics (Figure 3.6B). Mean age at maturity was linked to the third principal component (Table 3.2) and was positively correlated with the two species richness metrics

(Figure 3.6C). Length at maturity was the only metric linked to the fourth principal component.

3.4 Selection of the suite of surveillance metrics

In selecting a suite of metrics to act as surveillance indicators to monitor change in the general "health" of the North Sea's demersal fish community, a minimalistic approach might be adopted and only four metrics selected; one associated with each of the four principal components. However, the initial premise underlying selection of the 15 metrics used was that they represented five main attributes of the structure, composition and function of the demersal fish community. At least two of these attributes must co-vary if the 15 metrics can be reduced to four principal components. Examination of the linkages of the different metrics to the four principal components suggests that PC1 essentially covered the species evenness attribute, PC 2 was related to the abundance/biomass/productivity attribute, and PC3 corresponded to the species richness attribute; life-history trait and size composition did not actually emerge as distinct attributes of the structure, composition and functioning of the community.

One of the life-history trait metrics, mean length at maturity, was linked on its own with the fourth principal component. PC4 scores were the most variable over short time periods and revealed the least underlying trend. This principal component essentially portrayed the residual variation unexplained by the other three strongly trend driven principal components. It could be argued therefore that L_{Mat} might be discarded as a potential surveillance indicator because it was the least sensitive to any underlying trend. An alternative view might be that this metric should be retained precisely because it represents the residual unexplained variance in the community.

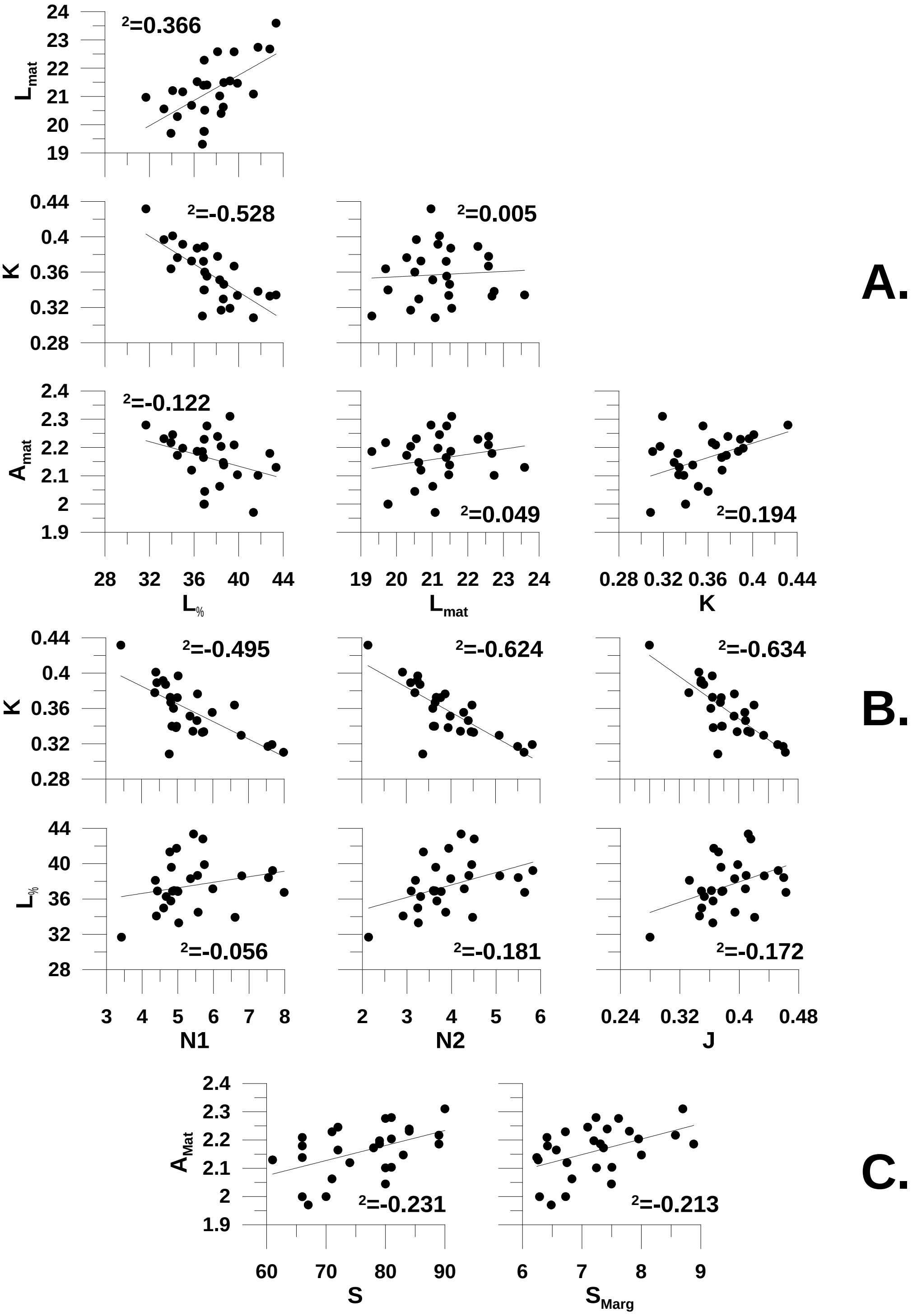

Figure 3.6. Correlations between: the four mean life-history trait metrics (A); the von Bertalanfy ultimate body length and growth parameter metrics and the three species evenness metrics (B); and mean age at maturity and the two species evenness metrics (C).

The two von Bertalanffy parameter metrics were linked to PC1 with the species evenness metrics, while the mean age at maturity metric was related to the species richness principal component. It could be argued that these three life-history trait metrics are redundant because they convey similar information to the species diversity metrics. However, the correlations were relatively weak (Figure 3.6); the life-history trait metrics do impart additional information. Furthermore, the relationships between the life-history trait and species diversity metrics were not entirely intuitive.

The metric trends suggested that when species evenness declined, the community was increasingly dominated by small-bodied fast-growing fish. When species richness increased, the average age at maturity of the community also increased. Monitoring the three life-history trait metrics as well as the species richness and evenness metrics, therefore potentially provides insight regarding the mechanisms that might be in operation. For example, immigration of dispersive species could be posited as an explanation for the increase in species richness that has occurred since the late 1980s. But such species tend to have r-strategy type characteristics, and are therefore unlikely to cause an increase in the average age at maturity in the resident community. The mean von Bertalanffy growth parameter had much the stronger correlation with the polynomial smoother fitted to the PC1 scores, and with the PC1 scores, suggesting that this metric was perhaps the more sensitive to any underlying trend. The suite of surveillance indicators could therefore be minimized, if necessary, by excluding the mean ultimate body length metric.

The two size composition metrics were only weakly correlated and linked to different principal components. The large fish indicator is the basis for the fish community EcoQO, and almost by definition therefore, this metric needs to be included in any suite of surveillance metrics. The LFI was negatively correlated with total abundance, total biomass and overall productivity of the demersal fish community. Because recovery of the LFI to a value of greater than 0.3, from a low of 0.05 in 2001, is the objective set for managers (Greenstreet *et al.* in review), this implies that corrective management will also be associated with a reduction in the total abundance, biomass and productivity of the demersal fish community. This argues for the retention of at least one of the three abundance/biomass/productivity metrics as well as the LFI. Mean weight of fish in the community was generally less sensitive to any underlying trend, and given the inclusion of the LFI, this metric could probably be excluded from a suite of surveillance metrics with relatively little loss of relevant information. Indeed ICES has already recommended that this not be used to support an EcoQO for the North Sea demersal fish community because of its sensitivity to environmentally driven recruitment events, which tend to add noise to univariate metric trends and obscure any underlying trend signal (ICES 2007a; 2007b).

Data in Tables 3.3 and 3.4 and the fits of the original metric values to polynomial smoothers (Figure 3.1) were used to determine which metrics should be selected from the main species evenness, abundance/biomass/productivity, and species richness attribute metrics associated with PC1, PC2, and PC3 respectively. For the PC1 metrics, Table 3.4 and the polynomial smooth fit to the original data selected Hill's N1, while the Table 3.3 fits selected Hill's N2. Essentially either metric could serve, but N2 might be more appropriate if control of sampling effort bias was an issue. For the PC2 metrics, abundance performed the best except for the fit of the original data to the principal component scores where overall productivity had marginally the stronger correlation. For the PC3 metrics, the analyses summarized in Table 3.4 suggested that Margalef's species richness metric performed marginally better than the simple species count. However, the polynomial smoother fitted to the original data suggested that the species count was slightly less noisy (Figure 3.1) and, in both cases, agreement between the original metric data and the third principal component scores, or the smoother fitted to these scores, was closest for the simple species count metric. On balance the simple species count metric is probably the best choice to include in any suite of surveillance metrics. But again, if sampling effort limitations were to compromise this metric (Greenstreet and Piet 2008), then S_{Marg} might after all be the better choice.

The analyses presented here suggest that the demersal fish community is characterized by three distinct structural or functional attributes: (1) overall abundance, biomass and productivity; (2) species richness; and (3) species evenness. These attributes condense down to essentially the number of individuals in the community, the number of species in the community, and the relative distribution of individuals between species. Variation in these main attributes showed distinct underlying temporal trends that differed from each other. Variation in these community structural attributes either influenced, or was influenced by, variation in what might be considered to be attributes of the individuals that comprised the community: the size of individuals in the community, and their life-history characteristics. Table 3.5 presents the final selection of metrics that might therefore best represent change in these characteristics of the North Sea demersal fish community over time, and therefore act as surveillance metrics to monitor variation in the general health of the demersal fish community of the North Sea.

Table 3.5. Surveillance metrics for the North Sea demersal fish community.

	COMMUNITY ATTRIBUTES	INDIVIDUAL ATTRIBUTES
First principle component	Total abundance	Large fish indicator
Second principle component	Hills N1 species evenness	Mean von Bertalanffy growth parameter
Third principle component	Species richness	Mean age at maturity

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4 Methods for comparing and summarizing fish and fish community distributions in relation to environment and habitat

ToR c) Further develop and explore mapping and other methods for comparing and summarizing fish and fish community distributions in relation to environment and habitat

4.1 Introduction

Mapping provides a powerful suite of tools for the presentation, interpretation, and analysis of spatially explicit data, enabling the formation of hypotheses, testing of predictions, and display of multidimensional and derived statistics. Often, real data are patchy in their temporal and spatial coverage of a system. Due to sampling bias and to survey methodology, the data provide an imperfect and often highly noisy summary of the real world. Due to logistical, technical and financial constraints, missing values may compromise temporal and/or spatial coverage. Thus, mapping techniques can be of value in smoothing local-scale noise and interpolating between data points to facilitate the characterization of large-scale patterns.

Trawl data are a very noisy representation of the true assemblage and by using single trawls to derive patterns, there is a danger of drawing unlikely conclusions. For example, the observation of a single predation hot spot, based on data derived from one haul, presented the possibility that predation by grey gurnard on juvenile cod might be so intense that the cod stock might never recover. (Temming *et al.*, 2007).

Maps can also be used to compare multiple layers to determine factors that relate to response variables. For example, bottom temperature, topography and seabed classification maps have been used to predict the likely distributions of marine fish and benthic invertebrate distributions (Kulka *et al.*, 2004; Moore *et al.*, 2009; Tremblay *et al.*, 2009; Greenstreet *et al.*, 2010). Models can also be derived using layers of data or maps, tested and revised using layers of data from other sources. Thus, one can drill down through the layers, then build up to make predictions.

4.2 Statistical methods for smoothing and interpolating spatially explicit data

Many models used to examine spatial distributions are problematic in terms of dealing with the statistical distribution of observations of count data. For example, kriging assumes a normal error distribution, a requirement often satisfied by modelling log (survey catch) rather than survey catches directly. This introduces a problem when empty hauls occur as the log of zero is not defined. Adding a constant to all catches does not remove the problem as the choice of the constant added now affects the results. Here we introduce two methods that can be used to avoid this issue.

The first approach uses a model designed to handle count-data, such as the Log Gaussian Cox Process (LGCP) (Lewy and Kristensen, 2009). This model uses untransformed data along with the observed spatial correlation to predict and interpolate unobserved densities at any location in the area. Being a likelihood-based method, the statistical testing of the effect of different explanatory variables (i.e. temperature) on density is straightforward.

The second approach is to use a method called potential mapping (SPANS, Intera), which works independently of the statistical distribution of the data (see example below). By encircling each point and assigning the value of the point to the circle, this method creates a large number of crescents created by the intersection of the circles, each with a value representing the average of the intersections. These crescents can then be categorized to produce a surface of values that are derived from the raw data but for spatial analyses provide more power for detecting large-scale patterns and trends. Examples are provided below.

4.3 Examples of mapping providing evidence that explains patterns

Eastern and western North Atlantic (refer to ICES, 2006, 2007 and 2008 for a description of potential mapping and matrix model overlays). Potential mapping is appoint to surface that is particularly useful for fisheries data in that it provides interpretable surfaces and handles various forms of geo-referenced data, grid data, random stratified, random etc. (Kulka and Pitcher, 2001). Modelling functions in SPANS add value with routines that allow multiple surfaces and point and surfaces to be overlaid. It also allows spatial variance to be mapped. To illustrate this procedure, Figure 4.1 that shows the difference in bottom temperatures on the Labrador Shelf in warm (July-November) and cold (December-June) months. The surfaces were created from point observations collected during research surveys. Such a surface can then be overlaid with fish distributions and/or other environmental attribute to model habitat associations based on different sets of data (for example, Kulka *et al.*, 2005). Another example shows how bycatch of different species in a fishery can be spatially compared by overlaying. For this example, we look at the bycatch of cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) in the yellowtail flounder (*Limanda ferruginea*) fishery on the Grand Bank (Kulka 2009). Here, abundance of the two bycatch species is very low and a spatial (and temporal) strategy is required to reduce the bycatch. Figure 4.2, the result of a matrix model overlay of geo-referenced cod and plaice bycatch catch rates shows where low (and high) bycatch rates of the two species coincides (Figure 4.2, green areas correspond to where bycatch rates of both cod and plaice are low, optimal areas to fish if bycatch reduction is a management objective). Thus, with this spatial information, a strategy can be formulated to reduce cod and plaice bycatch by shifting effort to locations where the bycatch of the two species is lower and catch rates of the target species is sustainable.

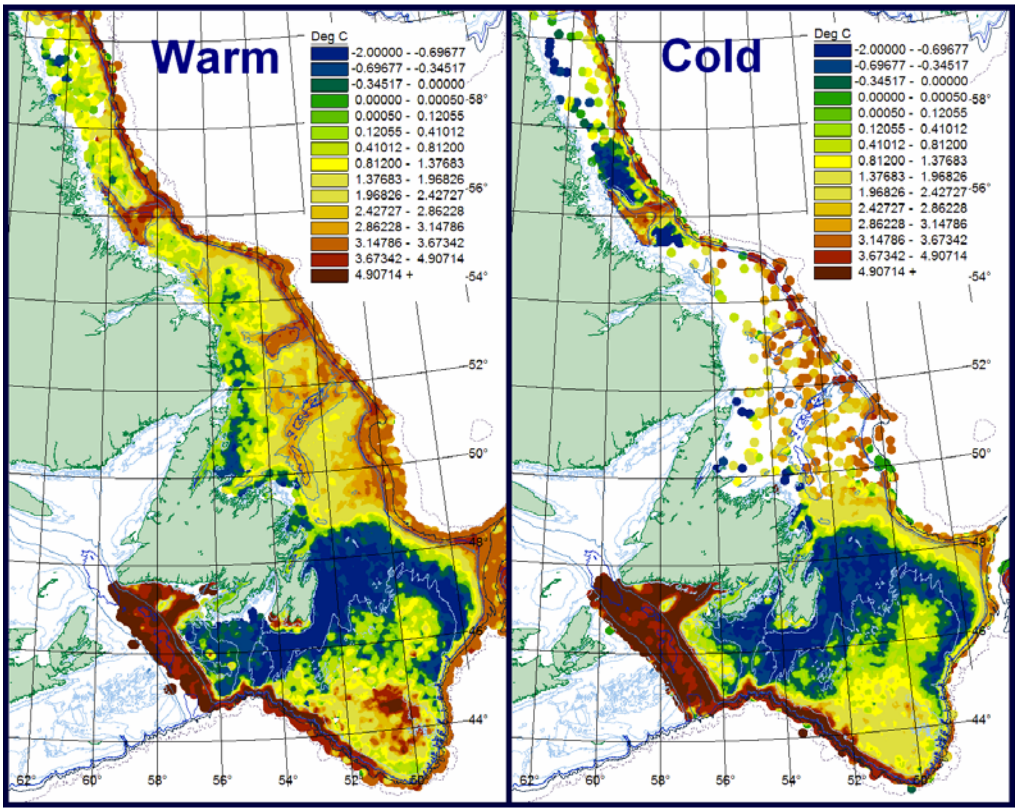


Figure 4.1. Long term (1977–2004) bottom temperature off Canada, interpolated, warm=July-November, cold=December-June. Created by potential mapping from bottom temperature point data to create a surface.

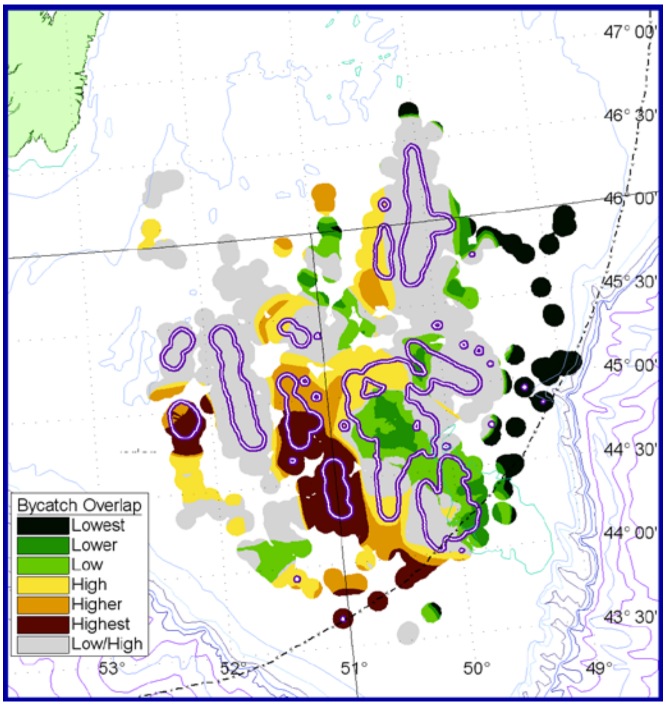
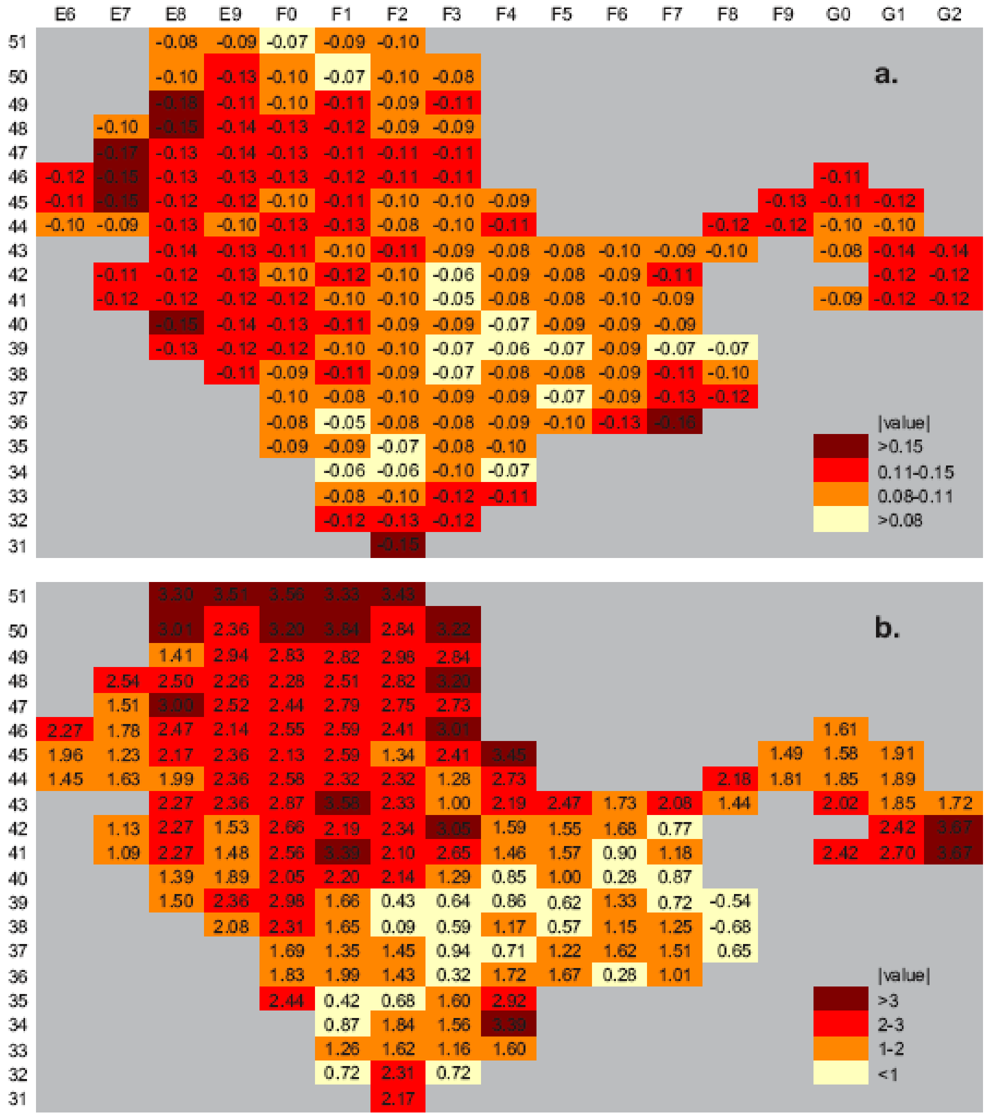


Figure 4.2. Cod/plaice matrix overlay for all years, 2000–2008 where cod and plaice catch rate surfaces are overlaid (refer to Kulka 2009). Brown, orange and yellow areas correspond to where the bycatch of both plaice and cod are high (for example, brown to yellow: plaice > 0.9979 and cod > 0.01557 t/hr). Green areas are where bycatch of plaice and cod are lowest. Overlaid lines encompass the major fishing grounds for yellowtail flounder on the Grand Banks.

Maps have also been used to represent patterns in metrics for fish populations. For example, Daan *et al.* (2005) calculated length–frequency metrics for North Sea fish, and through mapping, identified coherent patterns across much of the North Sea with regional-scale trends that would not be obvious without the use of mapping (Figure 4.3).



	E6	E7	E8	E9	F0	F1	F2	F3	F4	F5	F6	F7	F8	F9	G0	G1	G2
51			-0.08	-0.09	-0.07	-0.09	-0.10										
50			-0.10	-0.13	-0.10	-0.07	-0.10	-0.08									
49			-0.16	-0.11	-0.10	-0.11	-0.09	-0.11									
48		-0.10	-0.15	-0.14	-0.13	-0.12	-0.09	-0.09									
47		-0.17	-0.13	-0.14	-0.13	-0.11	-0.11	-0.11									
46	-0.12	-0.15	-0.13	-0.13	-0.13	-0.12	-0.11	-0.11							-0.11		
45	-0.11	-0.15	-0.12	-0.12	-0.10	-0.11	-0.10	-0.10	-0.09					-0.13	-0.11	-0.12	
44	-0.10	-0.09	-0.13	-0.10	-0.13	-0.13	-0.08	-0.10	-0.11				-0.12	-0.12	-0.10	-0.10	
43			-0.14	-0.13	-0.11	-0.10	-0.11	-0.09	-0.08	-0.08	-0.10	-0.09	-0.10		-0.08	-0.14	-0.14
42		-0.11	-0.12	-0.13	-0.10	-0.12	-0.10	-0.06	-0.09	-0.08	-0.09	-0.11				-0.12	-0.12
41		-0.12	-0.12	-0.12	-0.12	-0.10	-0.10	-0.05	-0.08	-0.08	-0.10	-0.09			-0.09	-0.12	-0.12
40			-0.15	-0.14	-0.13	-0.11	-0.09	-0.09	-0.07	-0.09	-0.09	-0.09					
39			-0.13	-0.12	-0.12	-0.10	-0.10	-0.07	-0.06	-0.07	-0.09	-0.07	-0.07				
38				-0.11	-0.09	-0.11	-0.09	-0.07	-0.08	-0.08	-0.09	-0.11	-0.10				
37					-0.10	-0.08	-0.10	-0.09	-0.09	-0.07	-0.09	-0.13	-0.12				
36					-0.08	-0.05	-0.08	-0.08	-0.09	-0.10	-0.13	-0.16					
35					-0.09	-0.09	-0.07	-0.08	-0.10								
34						-0.06	-0.06	-0.10	-0.07								
33						-0.08	-0.10	-0.12	-0.11								
32						-0.12	-0.13	-0.12									
31							-0.15										

	E6	E7	E8	E9	F0	F1	F2	F3	F4	F5	F6	F7	F8	F9	G0	G1	G2
51			3.30	3.51	3.56	3.33	3.43										
50			3.01	2.36	3.20	3.84	2.84	3.22									
49			1.41	2.94	2.83	2.82	2.98	2.84									
48		2.54	2.50	2.26	2.28	2.51	2.82	3.20									
47		1.51	3.00	2.52	2.44	2.79	2.75	2.73									
46	2.27	1.78	2.47	2.14	2.55	2.59	2.41	3.01							1.61		
45	1.96	1.23	2.17	2.36	2.13	2.59	1.34	2.41	3.45					1.49	1.58	1.91	
44	1.45	1.63	1.99	2.36	2.58	2.32	2.32	1.28	2.73				2.18	1.81	1.85	1.89	
43			2.27	2.36	2.87	3.58	2.33	1.00	2.19	2.47	1.73	2.08	1.44		2.02	1.85	1.72
42		1.13	2.27	1.53	2.66	2.19	2.34	3.05	1.59	1.55	1.68	0.77				2.42	3.67
41		1.09	2.27	1.48	2.56	3.39	2.10	2.65	1.46	1.57	0.90	1.18			2.42	2.70	3.67
40			1.39	1.89	2.05	2.20	2.14	1.29	0.85	1.00	0.28	0.87					
39			1.50	2.36	2.98	1.66	0.43	0.64	0.86	0.62	1.33	0.72	-0.54				
38				2.08	2.31	1.65	0.09	0.59	1.17	0.57	1.15	1.25	-0.68				
37					1.69	1.35	1.45	0.94	0.71	1.22	1.62	1.51	0.65				
36					1.83	1.99	1.43	0.32	1.72	1.67	0.28	1.01					
35					2.44	0.42	0.68	1.60	2.92								
34						0.87	1.84	1.56	3.39								
33						1.26	1.62	1.16	1.60								
32						0.72	2.31	0.72									
31							2.17										

Figure 4.3. Spatial variation in average (a) slopes and (b) heights of the size spectra (mean ln-cpue1977e2000 vs. 10-cm size classes) in first-quarter IBTS (Daan *et al.*, 2005)

4.4 Climate Envelope Modelling: Analysis and Discussion

The main principle of biogeography is that climate exerts a dominant control over the natural distribution of species (Pearson and Dawson 2003). Thus, it is not surprising that changing trends in climate are observed as a direct cause of trends in species' range expansion and retraction (e.g. Quero *et al.*, 1998, Beaugrand *et al.*, 2002, Beare *et al.*, 2004, Perry *et al.*, 2005, Ling *et al.*, 2009) and in spatial structure of the distribution within the range of the species (i.e. ICES, 2008, Figure 2.4.). In view of predicted changes in climate, modelling techniques, such as bioclimate envelope modelling, have evolved to correlate changes in species distributions to climate variables, as well as linking these range expansions and retractions structural spatial changes within the range to a physiological response of a species to climate variables.

A '*bioclimate envelope*' (or '*climate space*') can be defined as a set of physical and biological conditions that are suitable to a given species (Box 1981, Huntley *et al.*, 1995, Carey 1996, Bakkenes *et al.*, 2002, Berry *et al.*, 2002, Pearson *et al.*, 2002, Cheung *et al.*, 2009). Having identified a species' climate envelope, the application of scenarios of future climate change enables the potential redistribution of the species' climate space to be estimated (Berry *et al.*, 2002, Cheung *et al.*, 2009). Bioclimate envelopes for single species at different life-stages can vary depending on the needs and requirements for survival of each stage. Understanding the habitat needs for different life-stages and the availability of such habitat can thus help to identify potential bottlenecks for populations under future climate scenarios (Rijnsdorp *et al.*, 2009).

Whilst the bioclimate envelope modelling approach is highly valuable in making predictions of habitat availability, some limitations are recognized. As for all models, predictions of bioclimate envelope models are sensitive to assumptions and uncertainties (Pearson and Dawson, 2003, Thuiller 2004, Pearson *et al.*, 2006). Factors contributing to these uncertainties are the lack of consideration of species and biotic interactions, species dispersal at different life-stages, evolutionary change and the underlying assumption that species distributions are in equilibrium with their environment (Pearson and Dawson 2003, Guisan and Thuiller 2005, Brooker *et al.*, 2006). Despite these shortcomings, bioclimate envelope modelling currently represents one of the few available quantitative tools for predicting potential ecological changes resulting from species' distribution shifts and validations of the model as a predictive tool have been promising (e.g. Araujo *et al.*, 2005). Models can be improved by incorporating critical physiological processes (e.g. Ling *et al.*, 2009), such as growth, which allow determination not only of habitat availability based on species tolerances, but also establishing estimates of the quality of that available habitat. Knowledge of the quality of new habitat arising from species range shifts or expansions is important for drawing conclusions on the impact (both positive or negative) of climate induced distributional changes on the population. With regards to commercially exploited fish populations, such knowledge is vital due to the combined and interactive effects of both climate and fisheries on fish populations and consequently the feedback effect of climate induced population changes on fisheries.

4.4.1 E. Self-Organising Maps and Neural Networks

The response of marine communities to one or more drivers depends on the strength of the drivers, the environment in which the community resides, and the identity, abundance, and dynamics of the sum components of the community. This presents numerous potential parameters or variables that may influence the response, making studies to investigate or predict the numeric response at a single location complex, ambiguous or impossible. As a result, a growing appreciation of the complexity and non-linearity of living and physical systems has led to a shift in emphasis away from obtaining quantitative descriptions of systems, towards trying to identify qualitative features and patterns (Richardson *et al.*, 2003). By studying the response of multiple communities through space, patterns in response can be identified and analysed to detect common trends that relate to driver conditions.

The analysis of multiple drivers and environmental data layers is often challenging, and so Self-Organising Maps (SOMs) have been developed as an applied mathematical tool to identify spatial locations where similar responses have taken place (see Richardson *et al.*, 2003 for a thorough introduction). In essence, this method is based on an artificial neural network (ANN), which is a computer algorithm that simulates the processing architecture of the brain, allowing parallel processing of information in a network of interconnected simple units or nodes (Figure 4.4). By this approach, the neural network "learns" patterns in the data rather than relying on predetermined routines, which means that it can solve non-linear problems of almost infinite complexity. The technique lends itself to data with missing values, very often the case with survey data, because the nodes placed in the ANN algorithm interpolate between the data. The ANN approach is also well suited to marine survey data in that it does not require prior knowledge or rely on assumptions about the data, such as normality or equality of variances (Chen and Ware 1999).

SOMs utilize an unsupervised (competitive) ANN where nodes "compete" to best represent the data; an approach that is ideal for pattern recognition and classification. As such, SOMs can take spatially explicit and complex non-linear multivariate data and summarize the major spatial patterns of variation into a defined number of classes within a series of two-dimensional maps. In a recent study, SOMs were used with spatially-explicit simulation output for the southern North Sea to give five spatially distinct classes which displayed internally consistent dynamic behaviour (Allen *et al*., 2007). SOMs have also been successfully applied to combined oceanographic remote-sensing data and biological survey data. For example, patterns in SST anomalies were investigated to explore the dynamics of Benguela anchovy recruitment (Richardson *et al*., 2003) and altimetry data has been combined with Namibian sardine recruitment data to identify causal patterns (Hardman-Mountford *et al*., 2003). Current research (Simpson *et al*., in prep.) is now combining data from (a) satellite remote-sensing, (b) physical *in situ* oceanographic surveys, (c) habitat classification and (d) long-term fisheries monitoring surveys, to investigate patterns in the response of the UK fish assemblage to fishing and climate change. By this approach, the use of SOMs could greatly improve the examination and characterization of species abundance and community response patterns during defined periods or environmental regimes and should allow for the explicit identification of regions and communities possessing similar properties that display characteristic and predictable patterns of response.

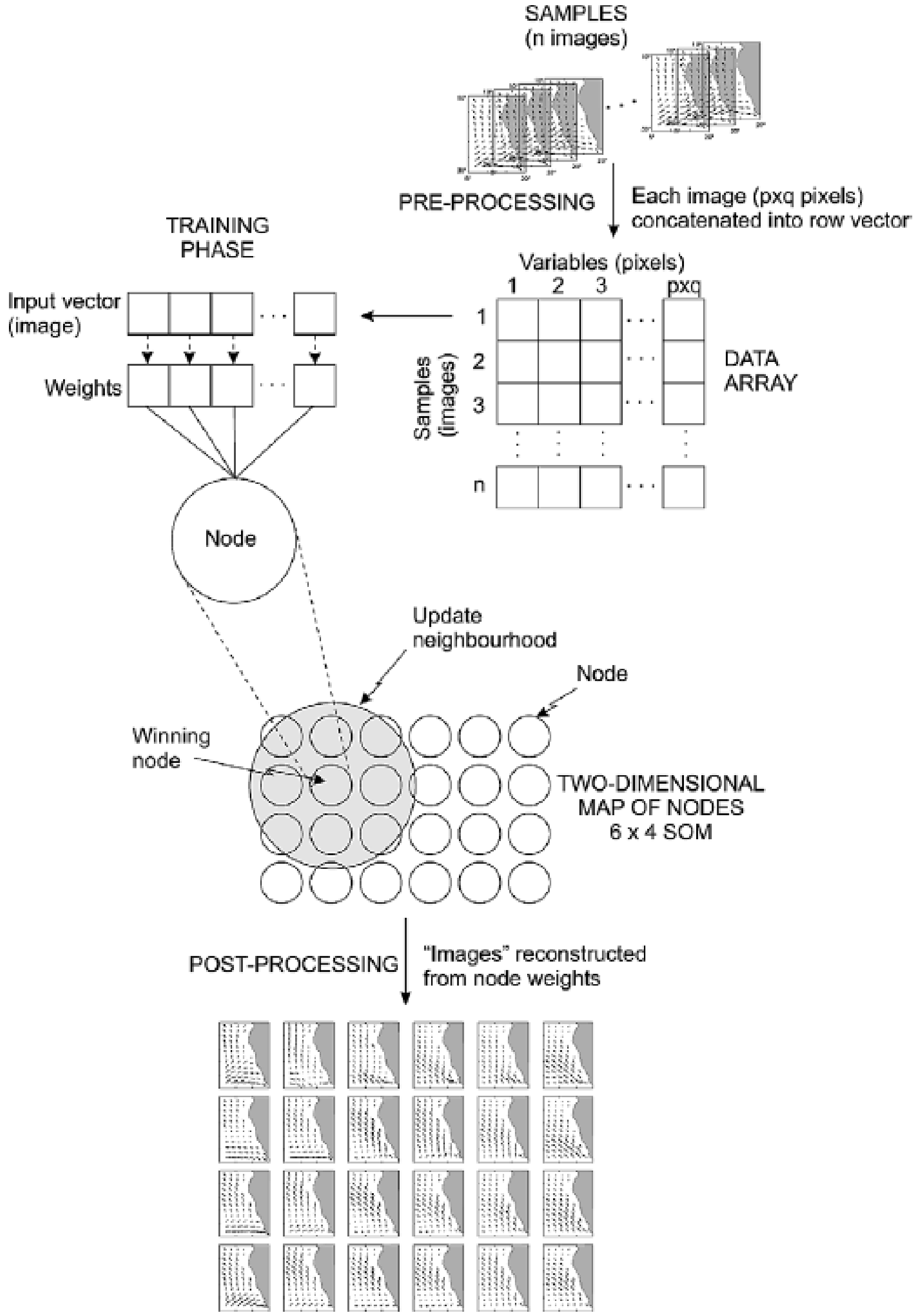


Figure 4.4. A schematic depicting the implementation of the self-organizing map, including the preprocessing, training, and post-processing phases (after Richardson *et al.* 2003).

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5 Abundance-Occupancy relationships: utilization of space by fish in relation to habitat, abundance, environment and exploitation

ToR d Under the umbrella of abundance/occupancy relationships and essential fish habitat:

i) Examine abundance occupancy relationships within species, and groups of species in different ecosystems in relation to habitat, environment and anthropogenic impacts

ii) Compare and contrast abundance/occupancy relationships and life-history characteristics for species common to NW and NE Atlantic (e.g. cod, haddock, spurdog, starry ray and herring)

5.1 Introduction

One approach to understanding community structure is to examine how populations within the community utilize potential habitat (space) as a function of the abundance of those populations. Abundance-Occupancy (A-O) relationships describe how individuals maintain distance between each other in relation to the total number of individuals and can be seen as a reflection of intraspecific competition combined with social and reproductive behaviours. A-O relationships are useful in that they provide a metric for assessing the status of individual species, community structure and resilience in response to natural or anthropogenic influences and this approach can be applied to individual species or at a community level (Gaston *et al.*, 2000).

Understanding A-O relationships are important because they may relate to the susceptibility of a species to random environmental fluctuations and spatially confined mortality processes such as habitat fragmentation or fishing. A species with an A-O relationship that strongly conserves local density would be susceptible to fisheries targeting aggregations. A-O relationships have been primarily fitted for single species and populations over time where there has been enough contrast in the abundance within the time-series to have some confidence in the fitted relationship. However, variation from the standard A-O relationship can also be fitted over multiple species within a system at a single point in time or over time. This resulting multispecies relationship may reflect community scale and spatial organizing (Holt *et al.*, 2002). Interspecific A-O relationships' should reflect competition between species as well as community response to external phenomena such as habitat fragmentation and loss (Donovan and Flather 2002, Freckleton *et al.*, 2006). For example, an analysis of a time-series of abundance and occupancy data for birds observed a weakening of the A-O relationship indicating a decoupling of community structure due to habitat fragmentation (Webb *et al.*, 2007). Clearly, changes in interspecific A-O relationships are likely to reflect either one or both of the changes in the community structure and habitat.

Previously, WGFE has devoted considerable effort to examining A-O relationships for several ecosystems including the Bay of Biscay, the Celtic Sea and Georges Bank. In the Bay of Biscay, strong abundance variations were observed; however, these changes were linked to occupancy for only a few species. In these cases, area occupied increased with abundance to a saturation level (high density) where no further area expansion was observed.

Intra- and interspecific occupancy-abundance relationships were also developed for the Georges Bank finfish and shellfish assemblage from 1963–2006 using data from the National Marine Fisheries Service's annual autumn bottom-trawl survey. Results indicated that the slope and strength of the interspecific (A-O) relationships significantly declined over the duration of the time-series. This decline in the quality of the fits and slope over species was significantly related to total groundfish landings. Breakpoint analysis of interspecific slopes indicated that 1973 was a period of "state" change. A "risk" assessment was developed to categorize a species' potential of increased catchability with changing abundance combined with a life history derived measure of population "resilience" (Frisk *et al.*, in press, Ecological Applications).

For 2009, WGFE was asked to address two topics on abundance-occupancy of fish:

i) Examine abundance-occupancy relationships within species, and groups of species in different ecosystems in relation to habitat, environment and anthropogenic impacts.

ii) Compare and contrast abundance-occupancy relationships and life-history characteristics for species common to NW and NE Atlantic (e.g. cod, haddock, spurdog, starry ray and herring).

Accordingly, in 2009 WGFE explored A-O relationships in Georges Bank fish in relation to potential habitat destruction and interpreted this in light of extinction debt theory (Tilman *et al.*, 1994). To address the second part of the request, species-specific A-O relationships were compared across several systems in the Northeast and Northwest Atlantic. Finally, new work was included where the potential bias in A-O relationships was determined as a function of number of individuals caught in survey hauls. This is a significant addition as surveys provide the data for all previous A-O relationships made in WGFE.

5.2 Does range size contraction signal an extinction debt caused by habitat destruction? - Georges Bank example

Malanson (2008) provides a comprehensive summary of extinction debt. The idea that geography interacting with ecological processes leads to the structuring of communities over time was developed in the late 1960s and 1970s (MacArthur and Wilson, 1967; MacArthur, 1972). Accordingly, an equilibrium number of species emerges, and is maintained by the balancing of inputs (immigration) and outputs (local extinction). The theory is often applied to colonization of unoccupied habitat, such as a new island, and was termed “island biogeography”. Early in the development of island biogeography, the importance of the time needed to reach equilibrium was recognized as was the importance of habitat fragmentation (Brown, 1971). Specifically, over time, habitat fragmentation can result in increased abundance of rapidly dispersing species and the local extinction of sedentary species (Diamond *et al.*, 1976). The extinction debt hypothesis by Tilman *et al.* (1994) introduced the counter-intuitive idea that the order of extinction with continued permanent habitat destruction would start with species that are the best competitors which are also usually the most abundant species in equilibrium conditions (Malanson 2008). At the same time, the poorer competitors but better dispersers or colonizers would increase in relative abundance. For example, if a community experiences habitat fragmentation and destruction, a “time delayed” extinction debt is realized that will result in the species with the greatest competitive ability and weakest colonizing ability to trend toward local extinction over multiple generations. The extinction debt hypothesis has been applied to habitat destruction for many terrestrial ecosystems and relatively few examples exist for marine communities. Our objective here is to apply the extinction debt hypothesis to the Georges Bank finfish and shellfish community from 1963–2006. Specifically, we will test if long-term declines in the A-O relationships observed on Georges Bank (Frisk *et al.*, in press) are consistent with the extinction debt hypothesis.

A-O relationships show that the total amount of habitat, its patchiness and connectivity are related to population size, spatial distribution and rates of exchange between habitats. For example, an analysis of a time-series of abundance and occupancy data for birds observed a weakening of the A-O relationship indicating a decoupling of community structure due to habitat fragmentation (Webb *et al.*, 2007). Clearly, destructive removal (trawling) of individuals and habitat fragmentation are fundamental to the strength and potentially, the shape of A-O relationships (Donovan and Flather 2002; Freckleton *et al.*, 2006). It is likely that changes in interspecific A-O relationships reflect either one or both of the changes in the community structure and habitat. While changes in community patterns are commonly observed, clear mechanisms are often not apparent or testable. A recent example was provided by Frisk *et al.* (in press) documenting a long-term decline in the strength and slope of the interspecific A-O relationship on Georges Bank. They found a significant and negative relationship between groundfish fishing effort and the strength and slope of the A-O relationship but were unable to test alternative hypotheses.

The present study examines the A-O relationship for the Georges Bank fish and finfish community as represented in the NOAA groundfish survey conducted each autumn since 1963. We examined the interspecific or multispecies (msAO) over time as well as the expected msOA (eAO) as a single curve fitted to all species and years combined. Our interest here was to examine the residuals of the eOA for temporal patterns that could indicate a systematic change in the nature of the A-O relationship that would be consistent with changes or potential losses in habitat and fragmentation and connectivity resulting from destructive trawling on George’s Bank. Our goal is not to describe the mechanism leading to the msAO and eAO. We accept that positive A-O relationships are all but inevitable (Hartley, 1998) and we sometimes fit a logit-log linear model not to capture specific mechanisms but because it models this inevitability. We do not impose ecological meaning on the fitted slopes and intercepts but examine the residuals for relationships in time with the assumption that these deviations from the model represent ecological phenomena. Furthermore, to strengthen our overall analysis, we include in our suite of fitting techniques non parametric spline fitting methods and examine residuals from these relationships.

5.2.1 Methods

Data

We analysed data from autumn National Marine Fisheries Service's (NMFS) bottom-trawl survey (autumn: 1963–2006). The survey utilized a Yankee 36 bottom trawl equipped with a 1.27-cm mesh liner (Sosebee and Cadrin, 2006). Stations consisted of tows 30 minutes in length at 1.95 m/s (Sosebee and Cadrin, 2006). The analyses herein only cover Georges Bank representing 40–100 stations per year. The NMFS selects stations based on a depth-stratified random design (Sosebee and Cadrin 2006). Species included in the analyses were those that were captured 1000 or greater times and were captured in at least 40 years, which amounted to 32 species in the dataset. This filtering procedure essentially selects for species that are both consistently sampled and those which are unlikely to be living on the edge of their range, are at low abundance (Bock and Ricklefs, 1983) and thus caught purely by chance.

Occupancy-Abundance relationships

Occupancy (O) for each species was estimated as the per cent of all stations with at least one individual present. Abundance (A) was estimated as the average annual number of fish captured per station (catch per unit of effort, CPUE). For fitting O-A relationships, we used an abundance minimum of 0.01 individuals/haul to exclude particular year-species combinations if they did not meet this criterion. Data were transformed to logit O and log A, for a more statistically correct means of fitting proportion data in O. A linear model was used to describe the O-A relationship:

$$\text{logit}(O) = s \log(A) + C$$

where, s and C are the fitted slope and intercept, respectively. In addition to the parametric model (eq. 1) we ran a model free cubic spline smoother though the transformed OA data. The advantage of the parametric model is that one can attempt to find ecological meaning in fitted parameters while this is not possible with the smoothed results. Our goal here though is to examine the residuals of the eOA and attempt to find meaning in them and this is possible for both methods.

The parametric model was fitted using two methods: generalized linear model assuming Gaussian distributed errors and reduced major axis regression which assumes errors in both dependent and independent variables. All models were fitted in the software R (R Development Core Team 2008). Residuals from the eOA determined from each of these methods were examined for temporal trends that reflect ecological meaning.

Segmented regression with a breakpoint analysis was performed on the time-series of the proportion of residuals that were positive to identify years where important changes in O-A occurred. This analysis was performed using the "strucchange" library in R. This method fits a series of linear regressions between breakpoints and parsimoniously optimizes the increase in quality of the overall fit of the segmented regression by penalising the fits by the number of breakpoints predicted in the series using the pseudo-Bayesian statistic Bayesian Information Criterion (BIC).

Species grouping criteria

For some analyses, data were subdivided into ecological groupings (Table 5.1) to examine the presence or absence of particular patterns within groups. Classification of species into groups was in some cases quite subjective while for other cases data could be used to inform the classification process.

Table 5.1. Ecological group assignment for each of the 32 Georges Bank species examined here. The complete species list and assignment to ecological groups can be found in Appendix 6.1

GROUPING	MEANING	EXAMPLE SPECIES
Growth group		
slow	slow growing, long doubling time (e.g. >8 years)	Redfish (*Sebastes spp*)
medium	between fast and slow	Cod (*Gadus morhua*)
fast	fast growing, doubling time <15 months	Butterfish (*Peprilus triacanthus)*
Trophic guild group		
benthivore	eats mostly benthic surface and infauna	Haddock (*Melanogrammus aeglefinus)*
planktivore	eats mostly in the plankton and nekton	Herring (*Clupea harengus*)
omnivore	eats many different food items	Cod (*Gadus morhua*)
piscivore	eats other fish	Dogfish (*Squalus acanthias*)
detritivore	Benthic scavenger, filter-feeder, deposit-feeder	lobster, scallop
Habitat group		
demersal	living near the bottom	Cod (*Gadus morhua*)
benthic	living on the bottom	American plaice (*Hippoglossoides platessoides*)
midwater or variable	often in midwater	Pollock (*Pollachius virens*)
pelagic	living mostly in the near-surface waters	Herring (*Clupea harengus*)
Mobility group		
Local	once settled tends to remain in an area (e.g. 20 km^2)	sculpins, scallop
medium	between local and wide	Haddock (*Melanogrammus aeglefinus)*
wide	very mobile, often makes long migrations	Mackerel (*Scomber scombrus*), dogfish (*Squalus acanthias*)
Colonisation group		
K	low fecundity, strong competitor	Skates (*Raja spp*)
Kr	between K and r	Yellowtail flounder (*Pleuronectes ferruginea*)
r	high fecundity	Squid (*Illex spp*)

5.2.2 Results

Deviations from expected relationship over time

The parametric models fitted to O-A data by GLM and RMA were not very different from each other, the GLM model producing lower slopes than the RMA (Figure 5.1, top panel). The spline smoother largely followed the RMA regression except at high abundance where the spline showed a flatter slope. Regardless of which model and method was used, the proportion of positive residuals by year decreased over the period from about 80% in the early 1960s to only about 30% around 2006 (Figure 5.1 bottom three panels).

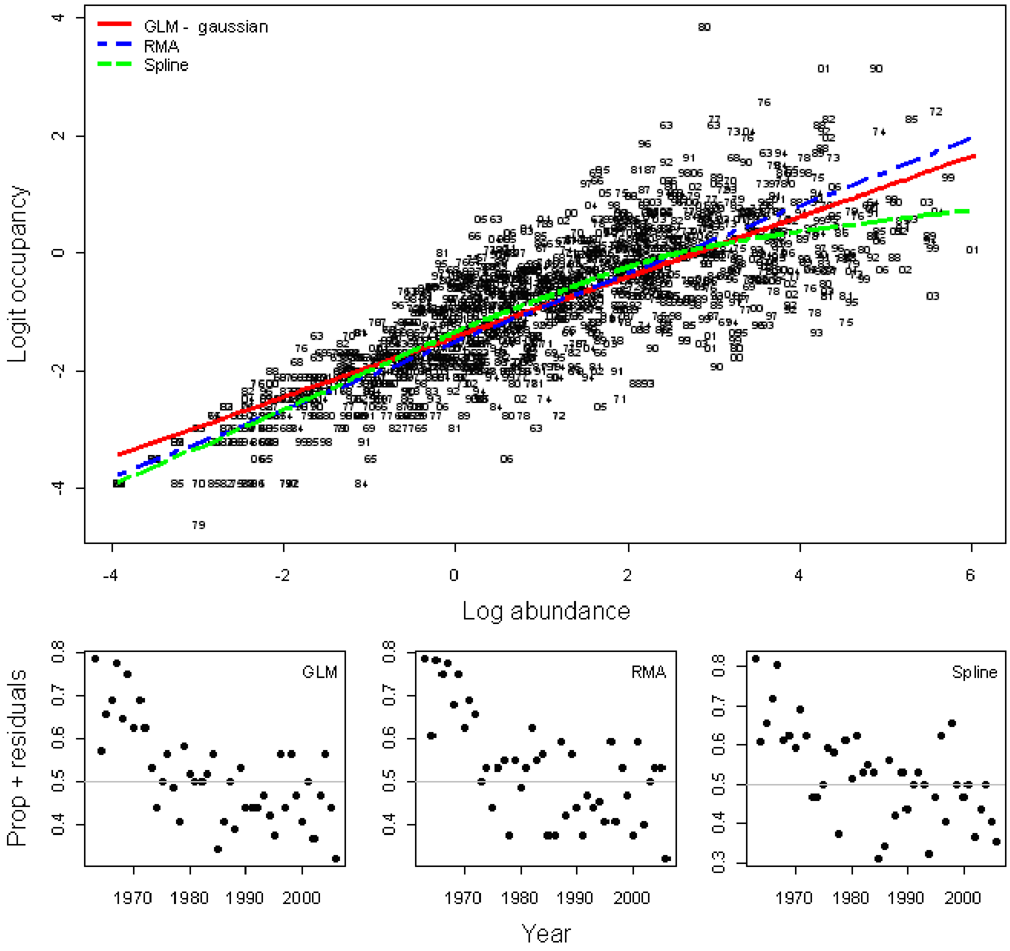


Figure 5.1. The expected occupancy-abundance relationship for Georges Bank fish through all data (1963–2006 and 32 species, n=1386), three methods are shown (top panel). Numbers as points in the top panel represent years. The three bottom panels show the proportion of the residuals from each of the three methods that were positive for each year. Note: residual patterns in the bottom panel do not indicate a violation of the O-A model fitting as the residuals are by year and not by the independent variable.

Applying a breakpoint analysis to both the GLM and RMA indicated a significant breakpoint in 1972 where residual deviations from the eOA switching from positive to negative (Figure 5.2). There was not a significant breakpoint in the temporal trends of the spline eOA, rather a decline over time from positive to negative residuals. It is notable, however, that the range in the proportion of the positive residuals was greater (0.31–0.82) compared to the GLM and RMA residual range (0.32–0.78). The model free spline approach produced an even greater contrast in the residual temporal trend.

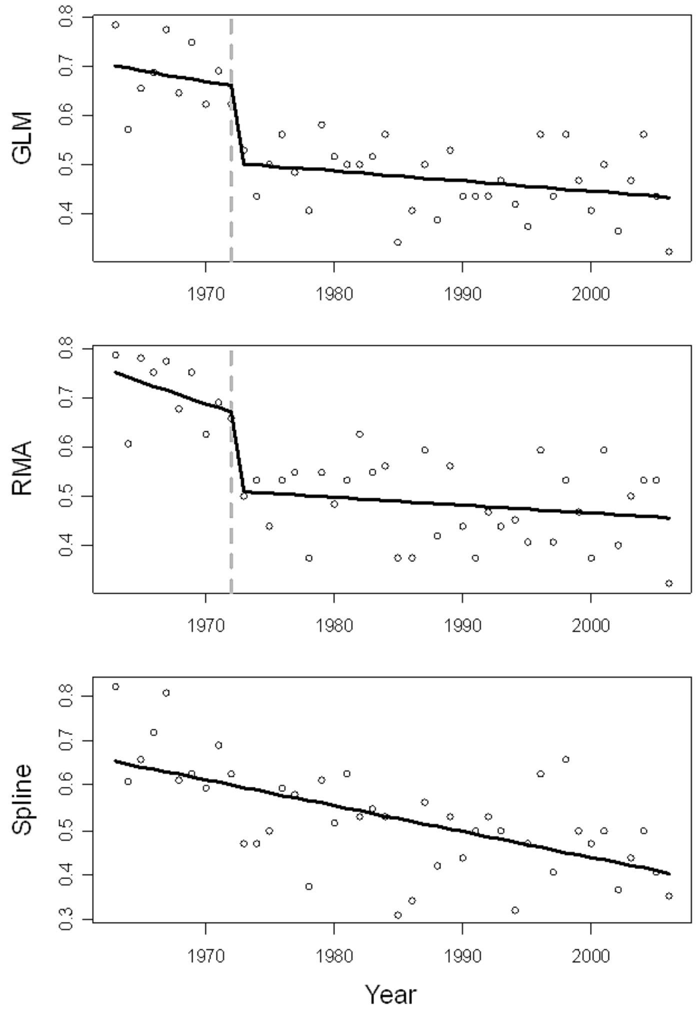


Figure 5.2. Breakpoint analyses performed on the proportion of positive residual time-series from the expected occupancy-abundance relationship determined by three different methods: generalized linear model (GLM), reduced major axis regression (RMA) and a cubit spline smoother (Spline). Significant breakpoints are depicted by vertical dashed lines at the breakpoint year and solid lines are the linear trends in periods between breakpoints.

The distribution of years over different abundance categories showed that the mean year for a category tends to be in the 1980s (analysis not shown here) while most categories contained both the first and last year of the time-series. The low and high abundance categories had the fewest number of species and thus the lowest potential to include at least one point from each year, thus there is no evidence that low abundance or high abundance values occurred predominantly in one period.

Analysis of residual pattern by species group

We examined the eOA for different ecological subgroupings of species to see if the community wide eOA and residual patterns over time could also be found in particular subgroups (Table 5.2). In most cases there was no residual pattern but in the cases where it was strong, this was in the categories containing more than 20 of the 32 species, weak relationship were sometimes found in groups with 14 or more species but there were no groups with fewer than 14 species where a residual pattern was found.

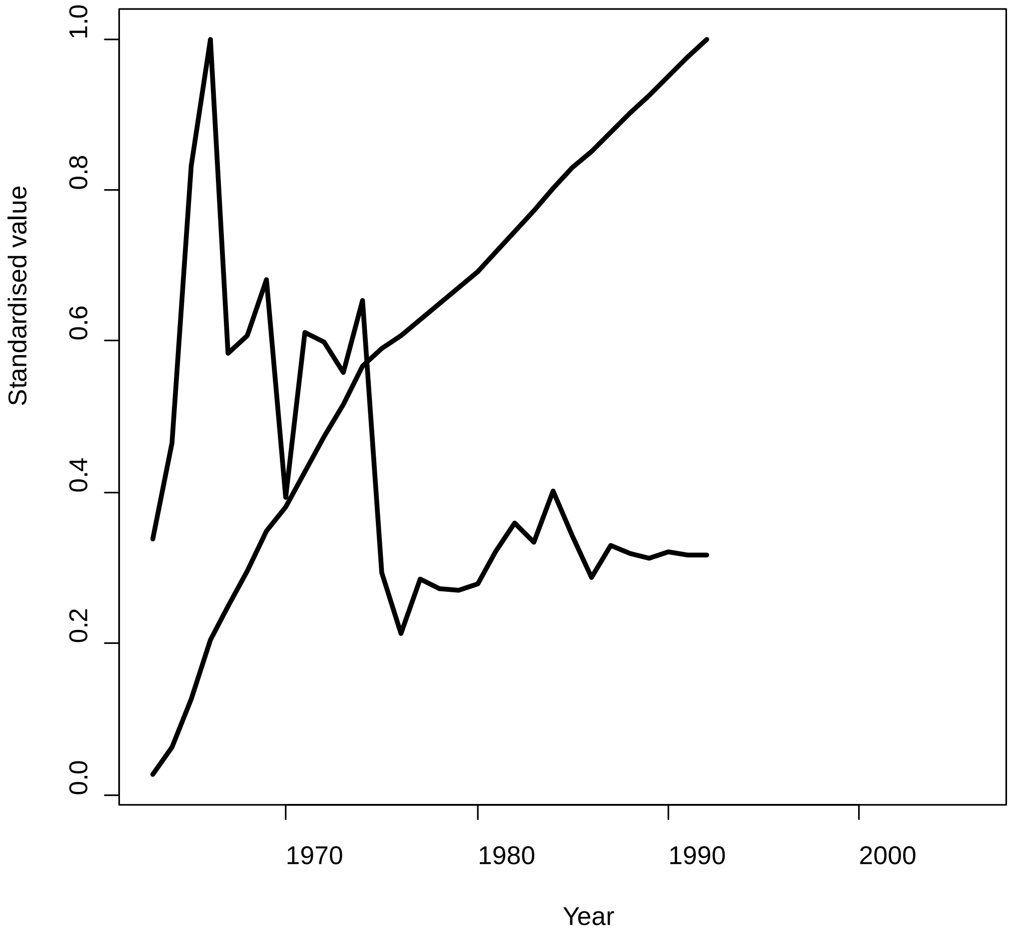
Thus, when groupings contained a large proportion of the community they tended to reflect the community temporal residual pattern, while no residual pattern was found in any ecological grouping category that did not have a large proportion of the species in the community.

Table 5.2. Temporal residual pattern of occupancy-abundance relationship residuals by various ecological groups of species. The residual pattern is classified as non-existent, weak and strong. A strong pattern would be similar to that found in the three bottom panels of Figure 1 while a "none" pattern appears as scatter about the 50% line regardless of year. N is the number of species in each group. Only groups with trends mentioned here.

		N	RESIDUAL PATTERN
Growth group			
	medium	21	strong
Trophic guild group			
	benthivore	20	weak
Habitat group			
	demersal	22	strong
Mobility group			
	medium	14	weak
Colonisation group			
	Kr	17	weak

Fishing effort and habitat destruction

We used cumulative trawling effort compiled for Georges Bank from 1963–1992 as an index of habitat destruction and fragmentation. Trawling effort was greatest in the 1960s until about 1967 which was determined as a breakpoint year (Figure 5.3). From 1968 to about 1973 trawling levels were fairly constant and the breakpoint analysis determined this to be an important change year where trawling slowed. From 1974–1981 trawling effort slowed again and thereafter it slowed until the end of the trawling time-series in 1992. The proportion of positive residuals was greater than 50% until about 1974 and thereafter decreased to between 40% and 50%. The proportion of positive residuals by the RMA and GLM methods both found significant breakpoints in 1972 similar to the 1973 found in cumulative trawling effort.


Standardised value
0.0
0.2
0.4
0.6
0.8
1.0
1970
1980
1990
2000
Year

and/or population extirpation given the deviations from the eOA that may be caused by fishing induced habitat fragmentation and destruction (Tilman *et al*., 1994).

Deviations from the eOA relationship clearly showed that during the beginning of the time-series, occupancy for any level of abundance was greater than expected while the opposite for later in the time-series. Further analysis of this showed that it could not be attributed to the change in the relative predominance of a certain categories of ecological grouping or the presence of low or high abundance years occurring late and early in the time-series respectively. This pattern thus seemed robust to some common artefacts of time-series analysis. Furthermore, two kind of linear model fitting and a smoothing spline and a variety of data transformation did not alter the temporal residual pattern, suggesting that this pattern was very robust. We are thus forced to question why species and populations would occupy fewer sites on George's Bank now than they did in the 1960s. A clear hypothesis could be that there are currently fewer sites with suitable habitat now than there used to be (Webb *et al*., 2007). In addition to habitat loss, there may have been loss of suitable habitat corridors and therefore increased habitat fragmentation (Donovan and Flather, 2002). We currently believe that this may be one of the most compelling hypotheses explaining the observed occupancy pattern. A strong alternative hypothesis could be that fishing has caused and maintains a local depletion pattern where individuals are kept in low abundance in certain areas such that they are not well sampled and thus population occupancy appears lower (Shackell *et al*., 2005). Though fishing likely contributed to our observed pattern, it is an insufficient explanation as our analysis of subgroups shows that the pattern does not necessarily occur in ecological groups that are the most heavily exploited and which are the one where we most likely expect the temporal deviation from the eOA to occur as fish landings increased over time (Gifford *et al*., 2009).

Tilman *et al*. (1994) described a theoretical model of species persistence in the face of habitat fragmentation and loss where the most competitive species was predicted to have the highest probability of extirpation essentially through recruitment attrition. Their modelling study is conditioned on the concept that dispersal and colonization ability are inversely related to competitive ability. This may be a more applicable concept in terrestrial environments where habitats are more easily identified and modes of dispersal usually a function of quantity (fecundity) and mobility. In marine environments, most fish have a relatively passive pelagic larval stage that is sufficiently long and they can be advected large distances by currents and thus dispersal may be less of an issue than in terrestrial systems. Nevertheless, the fecundity of fish can vary considerably and one might expect that the random passive aspect of larval movement would mean that fecundity could be a more important process. We also have examples of marine species which are both relatively slow growing K-like species which presumably are good competitors yet which are rather fecund. Monkfish, *Lophius americanus*, is a good example of this (Farina *et al*., 2008). Despite the differences between the Georges Bank fish community and Tilman's modelled community, the issue of extirpation and recovery of exploited fish stocks is so important in both Canada and the USA that both countries have legislated endangered species and precautionary management schemes for marine fish. We therefore need to seriously consider the possibility that current occupancy patterns of Georges Bank fish could be signalling an "extinction debt" or more aptly named future extirpation event.

Using trawling effort as an index of habitat destruction and fragmentation entails many assumptions. Though it is well known that bottom trawling by industrial fishing fleets can have profound and lasting influences on benthic habitats (Hiddink *et* *al.*, 2006; Thrush and Dayton 2002), we did not attempt to use effort as a strong quantitative explanatory variable. Apart from the non-trivial problem of deciding what constitutes a fish habitat, strong inference between habitat destruction and trawling effort would require information on the kinds of gears used, exactly where and when they were used as well as the destructive effect of a unit of effort. All that we can assume is that the cumulative impacts of trawling have negatively affected fish habitat and we therefore might expect a fish community response to this. Borrowing from the terrestrial literature (Freckleton *et al.*, 2006 ; Webb *et al.*, 2007) where habitat is much more easily defined and assessed, we hypothesized that total occupancy would decrease with habitat destruction. Indeed we found decreasing occupancy with cumulative trawling effort. It is important to interpret this result with caution because cumulative trawling cannot take account of habitat renewal that must have inevitably occurred over time in at least some areas of George's Bank. The question is how much renewal has taken place and if it would have been the kind of renewal that would have improved fish habitat and decreased fragmentation. It seems that because of the paucity of data on fish habitat or even what can be classified as fish habitat, we are unlikely to be able to answer these questions anytime soon. Nevertheless, we need to seriously consider the insights gained from terrestrial and theoretical studies suggesting that human disturbance that reduces habitat and increased fragmentation followed by decreased occupancy of populations can lead to an extinction debt. Even though we are far from quantifying this phenomenon and risk, recent international efforts to curb destructive fishing practices come none too soon (Gianni, 2004).

Our analysis of the residuals for breakpoints showing when the residual pattern changed considerably was found in the two parametric model fits in 1972 but there was just a continual decline in the occupancy for the spline fit residuals. 1972 was also the year when fish catches began to increase rapidly in response to increasing total production on George's Bank (Gifford *et al.*, 2009). This period also marks a point where species dominance increased and evenness decreased. The breakpoint in 1972 showing a large decrease in occupancy therefore further confirms that a community change occurred at this time. Together, the increasing dominance, declining diversity and occupancy spells a set of circumstance where a community could become much more vulnerable to perturbation such as fishing. That is, because fish are in more confined areas, there is lower species diversity and fisheries are taking more, then it signals the potential for a disproportionately large impact of fisheries on the community and many of the problems with changes in community composition and stock collapse in the late 1980s and 1990s could have arisen from these changes which occurred back in the early 1970s. Thus even back in the 1970s analyses of these phenomena may have foreshadowed the community impacts of fishing that would become apparent 15–20 years later. We should take this as a lesson for the present where occupancy seems only to be decreasing and we cannot be sure that there are not thresholds in occupancy that will signal unrecoverable debts.

The precautionary principle (PP) is essentially a reversal of burden of proof such that one needs to seriously consider possible impacts rather than consider only proven impacts. Here we have shown that there is occupancy contraction in George's Bank fish, what has caused this is not clear; however, because we need to adhere to the tenets of the PP we should consider the possible implications of this. Reduced occupancy could signal future extirpation of some species, also it make populations more vulnerable to activities such as fishing. We also need to consider metapopulation theory which describes a "rescue effect" of populations in fragmented landscape where increased occupancy means that the rescue effect is more likely to occur thus prevent extirpation of the total population (Holt *et al.*, 2004). We cannot show that that rescue effect is or is not occurring but we can infer that if fish habitats have been destroyed on George's Bank with increasingly fragmented remaining habitats, then population stabilizing phenomena like the rescue effect less likely to operate effectively and depensatory dynamics described the Allée effect are more likely to dominate (Stephens and Sutherland, 1999).

5.3 Comparison of abundance-occupancy relationships for species common to NW and NE Atlantic (e.g. cod, dogfish/spurdog, starry ray and herring

Changes in abundance may lead to changes in either area occupied, average density in occupied areas or a combination of the two. In the extreme, density in occupied areas can remain constant and an increase in abundance lead only to an increase in the area occupied. In the other extreme, the area occupied may remain constant while the density within the occupied area changes. All of three possible relationships between area occupied, density in occupied areas and abundance (density increase in occupied areas, increase in area occupied or increase in both) have been reported in the literature. However, it remains unclear whether the differences seen reflect consistent relationships for a given species or consistent relationships between species in a given area. To investigate this, the average catch in non-zero tows and the proportion of non-zero tows were estimated for 5 species occupying at least three of the areas for which survey data were available (Table 5.3). The relationship between abundance in occupied areas and the proportion of areas occupied is unlikely to be linear, as the proportion is bound to be in the interval between 0 and 1. To achieve a more linear relationship, the proportion of the non-zero hauls, p, was logit transformed before performing the subsequent analyses (logit=log (p/(1-p))). Further, to assure that variance did not increase with mean catch in non-zero hauls, the mean catch was log transformed. The relationship between the proportion of non-zero catches and mean catch in non-zero hauls of the five species can be seen in Figure 5.4.

There were clearly large differences between areas in the relationship for herring and plaice (Figure 5.4). In contrast, the relationships seen for starry ray were much more similar between areas. For cod, there appeared to be a lower mean density in occupied areas at a given occupancy than in the other areas whereas mean density in occupied areas of the northern Gulf of St. Lawrence was higher at a given occupancy than in the other areas. This effect may either reflect genuine differences or a difference in the proportion of the survey hauls conducted within potential cod habitat. If for instance 20% of the hauls were taken outside cod habitat, the maximum occupancy would be 80% and occupancy would appear to be lower at a given density in occupied areas. Similar considerations apply to the results for European plaice.

The logit of p and mean catch in non-zero hauls were significantly positively correlated in 15 of the 23 cases analysed (Table 5.4). This reflected a difference between species – all but one relationship were significant for herring whereas only one relationship was significant for plaice. There was no relationship between mean catch and correlation as would have been expected if the results were caused entirely by bias (see section 6.3, P(correlation=0)=0.86). When testing the slopes of the relationships for differences in a GLM (log(catch in non-zero tows) as dependent value due to the higher variance of this variable), only the slopes estimated for cod were significantly different between areas (P=0.0029). This was caused by a slope not significantly different from zero in the Bay of Biscay/Celtic Sea, Grand Banks in the Engels trawl and at Georges Bank. For the other species, a single slope could be estimated across all areas and only the intercept varied between areas. When estimating the slope over all areas, the difference between species was highly significant (P<0.0001) and all showed significant relationships between occupancy and density in occupied areas (P<0.0364, Table 5.5).

Table 5.3. Species and areas investigated for relationships between area occupied and density in occupied areas.

SPECIES	SCIENTIFIC NAME	AREAS
Starry ray	*Amblyraja radiata*	Northern Gulf of St. Lawrence, North Sea, Grand Banks, Georges Bank
Atlantic herring	*Clupea harengus*	Northern Gulf of St. Lawrence, Bay of Biscay/Celtic Sea, Eastern Channel, North Sea, Georges Bank
Atlantic cod	*Gadus morhua*	Northern Gulf of St. Lawrence, Bay of Biscay/Celtic Sea, Eastern Channel, North Sea, Grand Banks, Georges Bank
European plaice	*Pleuronectes platessa*	Bay of Biscay/Celtic Sea, Eastern Channel, North Sea
Spurdog	*Squalus acanthias*	Bay of Biscay/Celtic Sea, Eastern Channel, North Sea, Georges Bank

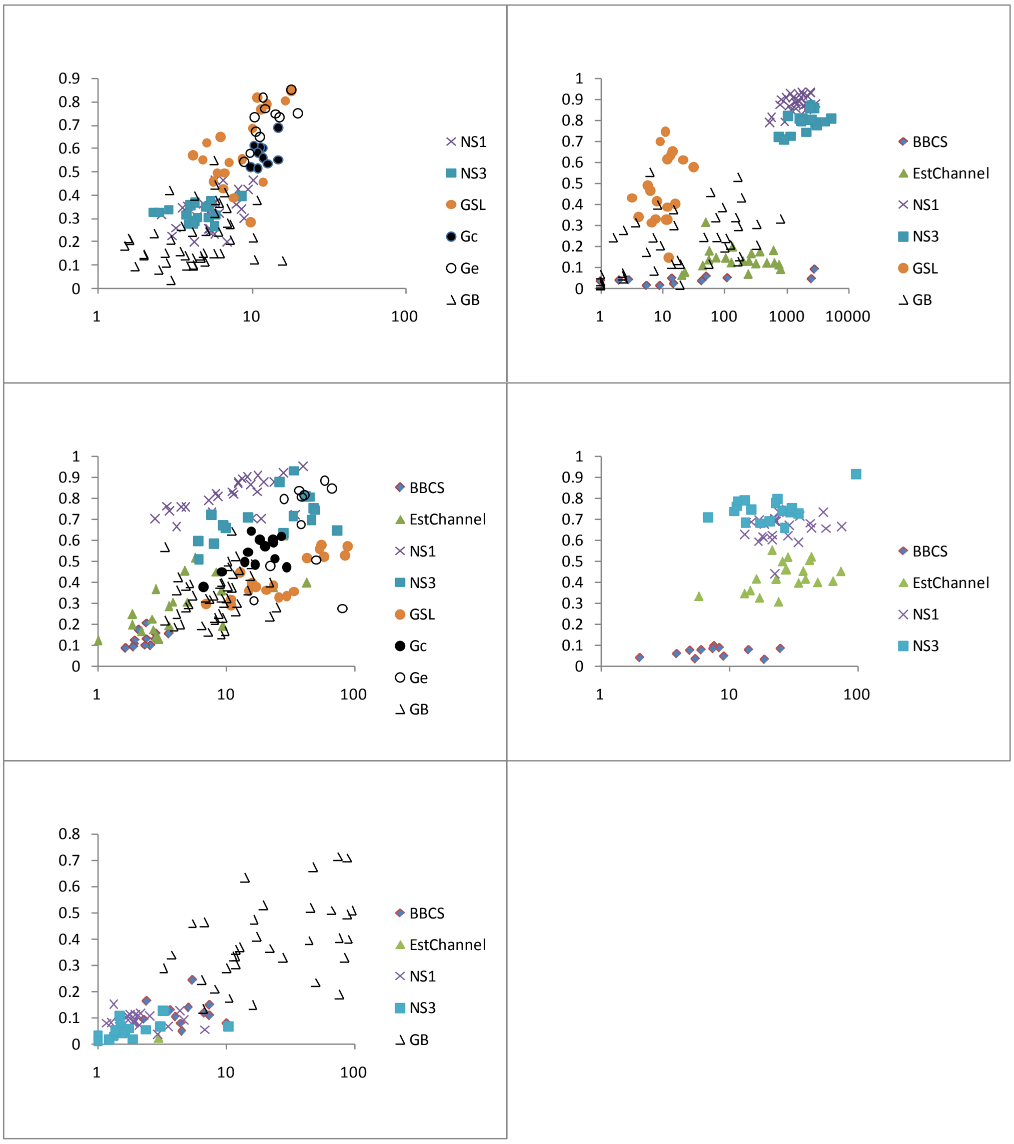


Figure 5.4. Relationship between logit (proportion of non-zero samples) and average catch in non-zero samples in different areas: BBCS: Bay of Biscay/Celtic Sea, EstChannel: Eastern Channel, NS1: North Sea quarter 1, NS3: North Sea quarter 3, GSL: Northern Gulf of St. Lawrence, Gc: Grand Banks Campelen, Ge: Grand Banks Engels, GB: Georges Bank.

Table 5.4. Correlation between the logit of occupancy and log (average catch in non-zero catches).

SPECIES	AREA	CORRELATION	P(CORRELATION=0)
Starry ray	Northern Gulf of St. Lawrence	0.559	0.0144
Starry ray	Grand Banks Campelen	0.400	0.3525
Starry ray	Grand Banks Engels	0.695	0.0185
Starry ray	North Sea Quarter 1	0.428	0.0158
Starry ray	North Sea Quarter 3	0.216	0.4203
Starry ray	Georges Bank	0.289	0.0148
Atlantic herring	Bay of Biscay/Celtic Sea	0.539	0.0486
Atlantic herring	Eastern Channel	0.052	0.8448
Atlantic herring	Northern Gulf of St. Lawrence	0.274	0.0449
Atlantic herring	North Sea Quarter 1	0.456	0.0421
Atlantic herring	North Sea Quarter 3	0.488	0.0348
Atlantic herring	Georges Bank	0.604	<0.0001
Atlantic cod	Bay of Biscay/Celtic Sea	0.483	0.0404
Atlantic cod	Eastern Channel	0.682	0.0024
Atlantic cod	Northern Gulf of St. Lawrence	0.832	0.0001
Atlantic cod	Grand Banks Campelen	0.818	0.1324
Atlantic cod	Grand Banks Engels	0.232	0.5682
Atlantic cod	North Sea Quarter 1	0.618	0.0069
Atlantic cod	North Sea Quarter 3	0.490	0.0081
Atlantic cod	Georges Bank	0.182	0.1056
European plaice	Bay of Biscay/Celtic Sea	0.191	0.5421
European plaice	Eastern Channel	0.450	0.0307
European plaice	North Sea Quarter 1	0.173	0.1563
European plaice	North Sea Quarter 3	0.544	0.3015
Spurdog	Bay of Biscay/Celtic Sea	-0.056	0.7891
Spurdog	Eastern Channel	0.388	0.0019
Spurdog	North Sea Quarter 1	0.030	0.8962
Spurdog	North Sea Quarter 3	0.541	0.0061
Spurdog	Georges Bank	0.501	<0.0001

Table 5.5. Species specific slope of the relationship between the logit of occupancy and log(average catch in non-zero catches)

SPECIES	SLOPE	P(SLOPE=0)
Starry ray	0.27	0.0339
Atlantic herring	0.91	<0.0001
Atlantic cod	0.59	<0.0001
European plaice	0.61	0.0364
Spurdog	0.61	<0.0001

5.4 Bias in the relationship between occupancy and abundance

Several authors have shown that the proportion of non-empty samples is intrinsically linked to the mean number of individuals per sample if individual distribution is random (Murawski and Finn 1988; Wright 1991; Hartley 1998). This reflects degree of aggregation where, for more highly aggregated species, there are fewer non-empty samples. Using the proportion of all samples containing more than a fixed density of individuals as a measure of area occupied does not solve the problem as this measure is also a direct function of mean density (Swain and Sinclair 1994). The bias takes the form depicted in Figure 5.5.

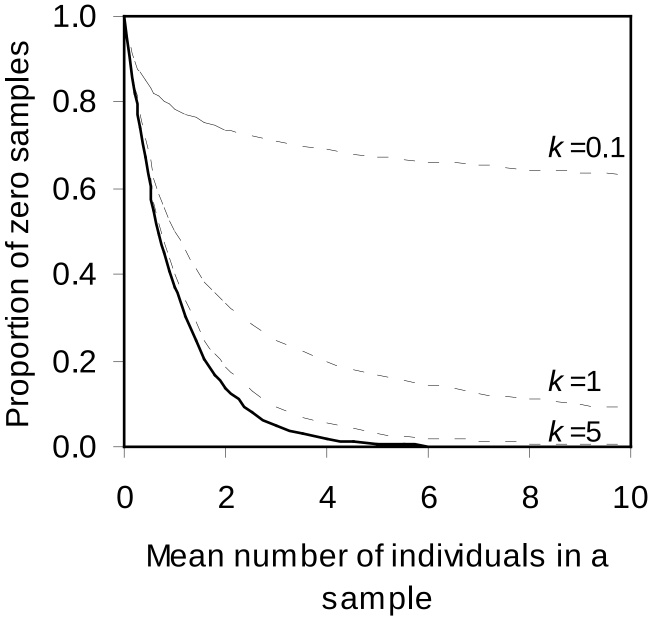


Figure 5.5. Relationship between proportion of empty samples and average number of individuals in a sample when individual are randomly distributed (Poisson, solid) and distributed according to a negative binomial distribution (hatched, different values of the size parameter *k*).

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5.6 Appendix 1. Species used in the Georges Bank occupancy-abundance analysis and their classification into different ecological groups which form the basis of sub-analyses

SPECIES	GROWTH GROUP	GUILD GROUP	HABITAT GROUP	MOBILITY GROUP	COLONISATION GROUP
Acadian redfish	slow	Ben	dem	loc	
American lobster	slow	Det	ben	loc	
American plaice	med	Ben	ben	med	
Atlantic cod	med	Om	dem	wide	
Atlantic herring	med	Plan	pel	wide	
Stlantic mackerel	med	Plan	pel	wide	
blackbelly rosefish	slow	Om	dem	med	
butterfish	fast	Plan	pel	wide	
fawn cusk-eel	fast	Ben	dem	med	
fourspot flounder	med	Ben	dem	med	
Gulf Stream flounder	med	Ben	dem	med	
Haddock	med	Ben	dem	med	
little skate	med	Ben	dem	wide	
longfin squid	fast	Pisc	pel	wide	
longhorn sculpin	med	Ben	dem	loc	
moustache sculpin	med	Ben	dem	loc	
northern sand lance	fast	Ben	dem	med	
northern shortfin squid	fast	Pisc	pel	wide	
ocean pout	med	Ben	dem	med	
Pollock	med	Pisc	mid	med	
red hake	med	Ben	dem	med	
sea raven	med	Ben	dem	loc	
sea scallop	med	Det	ben	loc	
silver hake	med	Pisc	mid	med	
spiny dogfish	slow	Pisc	dem	wide	
starry ray	slow	Ben	dem	wide	
white hake	med	Ben	dem	med	
Windowpane	med	Ben	dem	med	
winter flounder	med	Ben	dem	med	
winter skate	slow	Ben	dem	wide	
witch flounder	med	Ben	dem	wide	
yellowtail flounder	med	Ben	dem	wide	

6 Fish assemblages associated with offshore habitats (reefs, sandbanks, gas seeps) identified in the EU Habitats Directive

ToR e) Characterise the fish assemblages associated with offshore habitats (reefs, sandbanks, gas seeps) identified in the EU Habitats Directive.

6.1 Introduction

6.1.1 Background to the ToR

Council Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora (the Habitats Directive) is the means by which the European Community meets its obligations as a signatory of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). Each Member State is required to prepare and propose a national list of sites for evaluation in order to form a European network of Sites of Community Importance (SCIs). Once adopted, these are designated by Member States as Special Areas of Conservation (SACs). Natural habitat types of community interest whose conservation requires the designation of Special Areas of Conservation are listed in Annex I of the Directive. Of 189 habitats listed in this annex, only three occur in offshore waters (outside 12 nautical miles territorial seas) in the ICES area. These are;

- Sandbanks which are slightly covered by seawater all the time
- Reefs
- Submarine structures made by leaking gases

Further descriptions of these habitat types, including several sub-types, are given in European commission guidelines for the application of the Habitats Directive (European Commission Services 2007).

Under the Directive, Member States are required to *maintain or restore the natural habitats and the populations of species of wild fauna and flora at a favourable status* including the *natural habitat and its typical species.* However, there is no clear definition either in the text of the directive or the Commission's guidelines of what should be considered a "typical" species. Member States have differed conspicuously in their interpretation of the term "typical species", some regarding any species that has been recorded in a site as typical while others have drawn up much more conservative lists of typical species. In many cases, fish assemblages have not been directly addressed and this has caused difficulties when identifying suitable management measures. Commission guidelines list "characteristic species" for Annex I habitats however these vary considerably in the taxonomical level to which they are specified: for some habitats they list individual fish species whereas for others, they merely specify "various fish". There is clearly a need for consistent indicative lists of species that could be considered typical for each of the offshore Annex I habitats.

In considering this ToR, the working group concluded that it would not be possible for ICES to provide comprehensive lists of fish species associated with the broad habitat classifications listed in the Directive across the whole ICES area. Other factors, e.g. depth, latitude, hydrographic regime etc. are likely to be more important determinants of fish assemblage than benthic habitat alone. WGFE would therefore recommend that lists of typical fish species should be drawn up on a site by site basis based on the best available scientific evidence and, if necessary, dedicated surveys.

To assist the process of listing typical species for sites identified under the Directive, WGFE has briefly summarized available information on fish assemblages for each of the habitat types. A case study on fish assemblages of the North Norfolk Sandbanks, a prospective SAC in UK water of the North Sea, is included as an example of the type of study that would be required to describe typical fish species for an individual site. The Working Group does not consider that it will be possible to provide more definitive advice on this ToR at present.

6.2 Sandbanks which are slightly covered by seawater all the times

6.2.1 Definition of the habitat

European commission guidelines for the application of the Habitats directive define sandbanks as follows;

Sandbanks are elevated, elongated, rounded or irregular topographic features, permanently submerged and predominantly surrounded by deeper water. They consist mainly of sandy sediments, but larger grain sizes, including boulders and cobbles, or smaller grain sizes including mud may also be present on a sandbank. Banks where sandy sediments occur in a layer over hard substrata are classed as sandbanks if the associated biota are dependent on the sand rather than on the underlying hard substrata. "Slightly covered by seawater all the time" means that above a sandbank the water depth is seldom more than 20 m below chart datum. Sandbanks can, however, extend beneath 20 m below chart datum. It can, therefore, be appropriate to include in designations such areas where they are part of the feature and host its biological assemblages.

In the offshore environment, most of the sandbanks are elevated features arising from the seabed. A sandbank consists predominantly of sandy sediment mainly within a defined range of grain sizes larger grain sizes, including boulders and cobbles as well as smaller grain sizes, including mud, may be found on the sandbank, but only in small quantities.

For considering a sandbank as being a feature "slightly" covered by water, it has been decided to define the arbitrary depth of 20 meters below chart datum for the top of the sandbank: other parts of the feature may be found at deeper depths. Effectively, it is appropriate to also include sections of the sandbank extending below 20 m in depth where these are an integral part of the overall sandbank feature. Such features may cover a substantial area, and some of them have a trans-frontier dimension. The Dogger Bank in the North Sea is a typical case of a sandbank feature that extends across the marine zones of several Member States.

6.2.2 Characteristic species

The guidelines list the following as "characteristic species" for sandbanks;

Northeast Atlantic including North Sea: Invertebrate and demersal fish communities of sandy sublittoral (e.g. polychaete worms, crustacea, anthozoans, burrowing bivalves and echinoderms, *Ammodytes* spp., *Callionymus* spp., *Pomatoschistus* spp., *Echiichtys vipera, Pleuronectes platessa, Limanda limanda*).

Central Atlantic Islands (Macaronesian Islands): Fish, crustacean, polychaeta, hydrozoan, burrowing bivalves, irregular echinoderms.

Baltic Sea: Invertebrate and demersal fish communities of sandy sublittoral (fine and medium grained sands, coarse sands, gravely sands), e.g. polychaetes: *Scoloplus armiger, Pygospio elegans, Nereis diversicolor, Travisia sp.*, e.g. bivalves: *Macoma balthica, Mya arenaria, Cerastoderma sp.*, e.g. *crustaceans: Crangon crangon, Saduria entomon,* e.g. fish species: *Platichthys flesus, Nerophis ophidion, Pomatoschistus spp., Ammodytes tobianus.*

Mediterranean: Invertebrate communities of sandy sublittoral (e.g. polychaetes). Banks are often highly important as feeding, resting or nursery grounds for seabirds, fish or marine mammals.

6.2.3 A case study of the ichthyofauna of the North Norfolk Sandbanks

Sandbanks which are slightly covered by seawater all the time are listed on the EC Habitats Directive, and such habitats are widely distributed in European seas. Within UK waters (Figure 6.1), there are small areas of such habitat in the Irish Sea and elsewhere along the southern and west coasts, with the most extensive areas of this habitat in the southern North Sea (North Norfolk sandbanks) and central North Sea (Dogger Bank).

The North Norfolk sandbanks comprise a complex of linear sandbanks in the southern North Sea, extending from the Norfolk coast, ICES rectangle 34F1 out to ICES rectangle 35F2. The more inshore banks (Leman, Ower, and Well Banks) have extensive shallower areas, while the more offshore Broken Bank, Swarte Banks and Indefatigable Banks are deeper (Figure 6.2). For practical reasons, field studies (conducted in April 2006) focused on the Swarte and Broken Banks, as other banks were either too shallow for surveying by research vessel and/or had offshore gas installations and pipelines in the area.

The demersal fish (and epifauna) were sampled with a steel 2 m beam trawl with chain mat (see Jennings *et al.*, 1999 for a gear description). Tows were of 5 minutes duration with a warp:depth ratio of 3:1. Overall, 15 samples were collected for each bank, including five replicate samples (at one site) and four individual samples (four sites) along the crest of the bank, and single samples from three sites on either side of the bank. Larger epifauna and demersal fish were also sampled with two tows of a 4 m beam trawl between and parallel with the sandbanks.

Overall, 20 fish species were recorded during the survey (Table 6.1), although more species are likely to occur in the area. The use of additional fish sampling techniques (e.g. longline and gillnet) is required to determine which larger piscivorous fish may forage around offshore sandbanks. Several large-bodied piscivorous fish species (e.g. cod, spurdog, tope, turbot, bass) are taken in the general area, as shown by commercial landings data, and further studies to examine whether sandbanks are important feeding grounds or topographic features for such species are required.

The sandbank crests were typified by small catches of relatively few species, with the main species sampled including the invertebrates *Crangon crangon* and *Ophiura ophiura* and five species of fish: lesser weever *Echiichthys vipera*, solenette *Buglossidium luteum*, scaldfish *Arnoglossus laterna*, dab *Limanda limanda* and sand gobies *Pomatoschistus* spp. In contrast, sites in deeper water off the sandbanks were more speciose and the overall assemblages in these habitats were clearly different. The main differences between bank and off-bank habitats were caused by the high abundance of lesser weever and *C. crangon* on the crests of the banks, and larger numbers of species and increased abundance of species such as *O. albida, O. ophiura, L. holsatus*, sand gobies and solenette at off-bank sites (Ellis *et al*. In prep.).

In terms of demersal fish, lesser weever were more abundant on the crests of the sandbanks (mean catch per unit of effort = 39.3 ind.tow^{-1}) than at off-bank sites (0.6 ind.tow^{-1}). The length–frequency of lesser weever included a cohort of recently recruited fish (24–39 mm total length, L_T) as well as larger fish (ranging from 50–155 mm L_T), although the smaller size fish were only present from samples collected on the crests of the banks (Figure x.3). Catch rates of scaldfish were broadly similar in both habitats (3.9 and 2.8 ind.tow^{-1} on the sandbank and off-bank habitats), with fish ranging from 46–62 mm and 91–147 mm. The cohort of smallest fish was proportionally more abundant on the crest (23.9% of the total number of scaldfish caught on the sandbank) than at off-bank sites (14.7% of total individuals). Solenette were caught in greater numbers at off-bank sites than on the sandbanks themselves (53.7 and 14.6 ind.tow^{-1}, respectively), although the overall length distribution (30–117 mm) was comparable in both habitats. Although most solenette ranged from 60–105 mm L_T, there was also a cohort of fish 30–50 mm. Sand gobies were also more common on off-bank sites (15.3 ind.tow^{-1}) than on the crests of the sandbanks (1.9 ind.tow^{-1}), with a more restricted length range observed on the sandbank (39–56 mm) than from off-bank sites (32–72 mm).

The smallest cohort of lesser weever (24–39 mm LT) was recorded on the crest of the sandbank, but was not observed at off-bank sites. Given that lesser weever leave the plankton at 13–15 mm (Russell, 1976), these sandbanks may serve as an important nursery ground for this species. Other fish species for which early life-history stages were observed on the sandbanks included solenette (30–50 mm LT) and scaldfish (46–62 mm LT), and these species leave the plankton at approximately 10 mm and 16–30 mm, respectively (Russell, 1976). Further studies on the use of sandbanks by early life-history stages is required in order to determine whether there is increased recruitment to such habitats, with fish descending to deeper water as they increase in size. This would mimic the distribution pattern frequently displayed by many other juvenile fish species in coastal waters (Heinke's Law), but there is little evidence that this can operate so far offshore and over such a small scale.

Many of the fish and benthic species observed on the sandbanks are widely distributed in other sandy habitats on the continental shelf, and the fauna of sandbank communities may simply be based on a specialized niche of the sand-associated fauna of the region. None of the taxa observed in the study would seem to be obligate sandbank species and occur on other sandy habitats, as also reported in other regions (Kaiser *et al.* 2004). However, certain taxa (e.g. *E. vipera*) may be locally abundant and potentially indicative of such habitats.

Sandbank habitats may be an important habitat for lesser weever, as they bury into sandy sediments, and are ambush predators feeding on crangonids and other hyperbenthic crustaceans (Ellis, unpublished data). The presence of ambush predators on the tops of sand ridges has also been observed in the NW Atlantic, where species such as *Astroscopus guttatus* (Uranoscopidae) and *Trachinocephalus myops* (Synodontidae) are an important component of the sand ridge ichthyofauna (Vasslides and Able, 2008). The topographic features of sandbank habitats may create local hydrodynamic mechanisms that concentrate planktonic larvae (Ma *et al.,* 2006), which could explain both the importance of sandbanks habitats as settlement and nursery grounds, but also the abundance of those ambush predators that can retain their position in sites of potentially high velocity water movement by burying into the sediment.

Sandbanks are also topographically complex habitats, and further studies to examine the fine scale distribution and microhabitat use of certain species would clearly improve our understanding of the dynamics of the sandbank ecosystem. Indeed, certain species or life-history stages of fish may select specific microhabitats associated with sandy substrata (e.g. sand waves, ribbons, ripples, sand patches with emergent fauna), whether for shelter or trophic interactions (Auster *et al.,* 1995; 2003; Diaz *et al.*, 2003; Vasslides and Able, 2008).

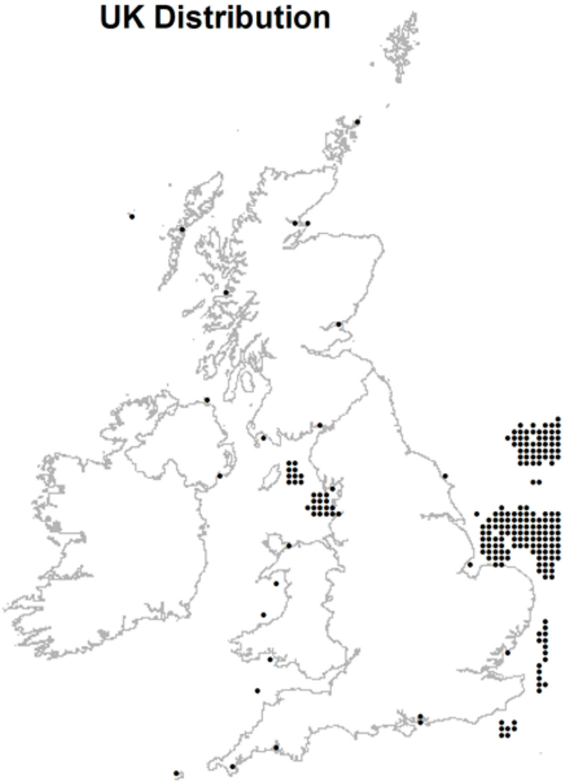

Figure 6.1. Distribution of "Sandbanks which are slightly covered by seawater all the time" (Source: JNCC, see http://www.jncc.gov.uk).

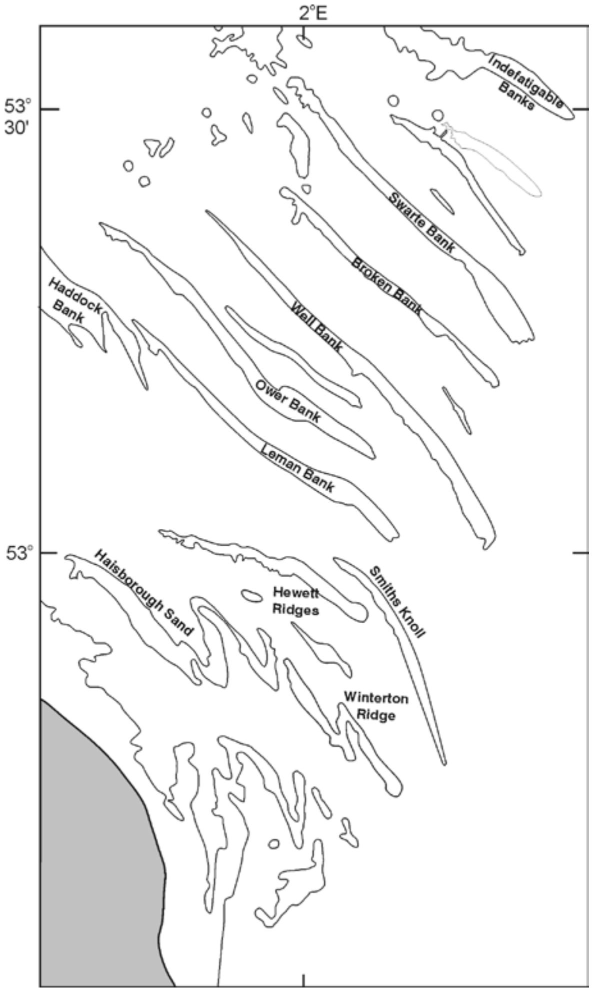

Figure 6.2. North Norfolk sandbanks.

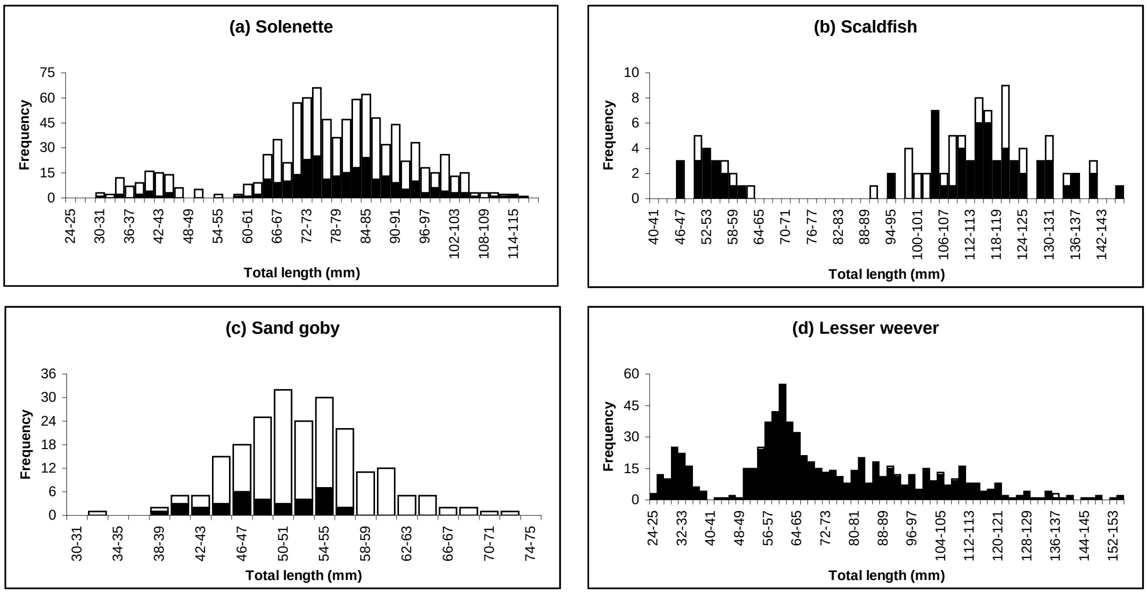

Figure 6.3. Length-frequency distributions (by 2mm length categories) for (a) solenette, (b) scaldfish, (c) sand goby and (d) lesser weever caught by 2-m beam trawl on the tops of sandbanks (black bars, 18 hauls) and from off-bank sites (white bars, 12 hauls).

Table 6.1. Taxonomic list of fish occurring on and around the North Norfolk sandbanks. Gears included 2 m beam trawl (T) and 4 m beam trawl (B).

FAMILY	SPECIES	GEAR
Rajidae	*Raja montagui*	B / T
Gadidae	*Enchelyopus cimbrius*	T
	Merlangius merlangus	B / T
Syngnathidae	*Entelurus aequoreus*	T
	Syngnathus acus	T
Triglidae	*Eutrigla gurnardus*	B / T
Cottidae	*Myoxocephalus scorpius*	B / T
Agonidae	*Agonus cataphractus*	B / T
Cyclopteridae	*Cyclopterus lumpus*	B
Trachinidae	*Echiichthys vipera*	B / T
Ammodytidae	*Ammodytes marinus*	Callaway *et al.* 2002
	Ammodytes tobianus	T
	Gymnammodytes semisquamatus	T
	Ammodytidae	B
Callionymidae	*Callionymus lyra*	B / T
	Callionymus reticulatus	T
Gobiidae	*Pomatoschistus sp.*	B / T
Scophthalmidae	*Lepidorhombus whiffiagonis*	Callaway *et al.* 2002
Bothidae	*Arnoglossus laterna*	B / T
Pleuronectidae	*Limanda limanda*	B / T
	Pleuronectes platessa	B / T
	Buglossidium luteum	B / T
Soleidae	*Solea solea*	B / T

6.3 Reefs

6.3.1 Definition of the habitat

European commission guidelines for the application of the Habitats directive define reefs as follows;

> *Reefs can be either biogenic concretions or of geogenic origin. They are hard compact substrata on solid and soft bottoms, which arise from the seabed in the sublittoral and littoral zone. Reefs may support a zonation of benthic communities of algae and animal species as well as concretions and corallogenic concretions. Clarifications: - "Hard compact substrata" are: rocks (including soft rock, e.g. chalk), boulders and cobbles (generally >64 mm in diameter). - "Biogenic concretions" are defined as: concretions, encrustations, corallogenic concretions and bivalve mussel beds originating from dead or living animals, i.e. biogenic hard bottoms which supply habitats for epibiotic species. - "Geogenic origin" means: reefs formed by non biogenic substrata. - "Arise from the seabed" means: the reef is topographically distinct from the surrounding seabed. - "Sublittoral and littoral zone" means: the reefs may extend from the sublittoral uninterrupted into the intertidal (littoral) zone or may only occur in the sublittoral zone, including deep-water areas such as the bathyal. - Such hard substrata that are covered*

> *by a thin and mobile veneer of sediment are classed as reefs if the associated biota are dependent on the hard substratum rather than the overlying sediment. - Where an uninterrupted zonation of sublittoral and littoral communities exists, the integrity of the ecological unit should be respected in the selection of sites. - A variety of subtidal topographic features are included in this habitat complex such as: Hydrothermal vent habitats, seamounts, vertical rock walls, horizontal ledges, overhangs, pinnacles, gullies, ridges, sloping or flat bed rock, broken rock and boulder and cobble fields.*

The guidelines list the following as "characteristic species" for reefs;

Northeast Atlantic including North Sea: In general, sessile invertebrates specialize on hard marine substrata such as sponges, anthozoa or cnidaria, bryozoans, polychaetes, hydroids, ascidians, molluscs and cirripedia (barnacles) as well as diverse mobile species of crustaceans and fish.

Central Atlantic Islands (Macaronesian Islands): Gorgonians, hydrozoans, bryozoan and sponges, as well as diverse mobile species of crustacean, molluscs (cephalopoda) and fish are characteristic.

Baltic Sea: Distribution and abundance of invertebrate species settling on hard substrata are limited by the salinity gradient from west to east. Typical groups are: hydroids, ascidians, cirripedia (barnacles), bryozoans and molluscs as well as diverse mobile species of crustaceans and fish.

Mediterranean: Cirripedia (barnacles), hydroids, bryozoans, ascidians, sponges, gorgonians and polychaetes as well as diverse mobile species of crustaceans and fish are characteristic.

6.3.2 Notes on the ichthyofauna of reefs in the ICES area

Fish assemblages on cold water coral reefs in the Northeast Atlantic have been described by various authors based on catches from longlines and gillnets (Husebø *et al.*, 2002) and trawl (Hall-Spencer *et al.*, 2002). However, in these studies, the presence of reef habitat was inferred from the occurrence of coral in the fishing gear. Underwater video, which has been used widely to identify and characterize reefs, provides greater confidence in the association of fish assemblages with reef habitat. (Mortensen *et al.*, 1995, Fosså *et al.*, 2002, Freiwald *et al.*, 2002 Costello *et al.*, 2005). This type of survey also has the advantage of being considerably less destructive to corals than trawl or longlines.

Costello *et al.* (2005) used a variety of underwater video methods to compare the fish associated with *Lophelia* reefs at 8 different locations in the Northeast Atlantic from the Sula and Tautra reefs in Norway, to the Porcupine Seabight off Ireland. Depths ranged from 39 m at the Tautra Reef to 1,015 m in the Porcupine Seabight. They found that the depth of the study sites was the most important factor related to the composition of the fish assemblages. Characteristic species were *Pollachius virens* at Tautra Reef (40 m depth), *Gadus morhua* at Kosterfjord (77–118 m), *Sebastes* sp. At Sula Reef (300–400 m) and *Synphobranchus kaupii* and Moridae at sites over 600 m dept. *P. virens* and *Trisopterus minutus*, wolffish *Anarhichas lupus, Sebastes* sp., and lotid *Brosme brosme* were most frequently recorded in association with the coral reef habitat. *Coryphaenoides ruprestris, G. morhua,* Macrouridae, *Trisopterus luscus,* and Moridae including *Lepidion eques,* were more frequently observed in the transitional zone (a mix of patches of coral over coral debris and seabed) and coral debris habitat. *Chimaera monstrosa, Notocanthus* sp., *S. kaupii*, and *Microstomus kitt* were more closely associated with sedimentary seabed habitat.

6.4 Submarine structures made by leaking gases

6.4.1 Definition of the habitat

European commission guidelines for the application of the Habitats Directive define Submarine structures made by leaking gases as follows;

> *Submarine structures consist of sandstone slabs, pavements, and pillars up to 4m high, formed by aggregation of carbonate cement resulting from microbial oxidation of gas emissions, mainly methane. The formations are interspersed with gas vents that intermittently release gas. The methane most likely originates from the microbial decomposition of fossil plant materials. The first type of submarine structures is known as "bubbling reefs". These formations support a zonation of diverse benthic communities consisting of algae and/or invertebrate specialists of hard marine substrata different from that of the surrounding habitat. Animals seeking shelter in the numerous caves further enhance the biodiversity. A variety of sublittoral topographic features are included in this habitat such as: overhangs, vertical pillars and stratified leaf-like structures with numerous caves.*
>
> *The second type are carbonate structures within "pockmarks". "Pockmarks" are depressions in soft sediment seabed areas, up to 45 m deep and a few hundred meters wide. Not all pockmarks are formed by leaking gases and of those formed by leaking gases; many do not contain substantial carbonate structures and are therefore not included in this habitat. Benthic communities consist of invertebrate specialists of hard marine substrata and are different from the surrounding (usually) muddy habitat. The diversity of the infauna community in the muddy slope surrounding the "pockmark" may also be high.*

Such habitats include, for example the Braemar and Scanner pockmarks, and the Gullfaks and Tommeliten methane seeps in the North Sea. These pockmarks are a series of crater-like depressions, of which some contain 'submarine structures made by leaking gases'.

6.4.2 Characteristic species:

The guidelines list the following as "characteristic species" for Submarine structures made by leaking gases;

"Bubbling reefs"

Plants: If the structure is within the photic zone, marine macroalgae may be present such as Laminariales, other foliose and filamentous brown and red algae. Animals: A large diversity of invertebrates such as Porifera, Anthozoa, Polychaeta, Gastropoda, Decapoda, Echinodermata as well as numerous fish species are present. Especially the polychaete Polycirrus norwegicus and the bivalve Kellia suborbicularis are associated species of the "bubbling reefs".

"Pockmarks"

Plants: Usually none.

Animals: Invertebrate specialists of hard substratum including Hydrozoa, Anthozoa, Ophiuroidea and Gastropoda. In the soft sediment surrounding the pockmark Nematodae, Polychaeta and Crustacea are present.

6.4.3 Notes on the ichthyofauna of methane seeps

At these sites, various types of methane-derived carbonate material have been deposited, and such carbonate structures provide a habitat for a fauna that comprises both specialised chemosynthetic organisms (e.g. microbes) that utilize methane and other by-products (Wegener *et al*., 2008), specialised invertebrates (Dando *et al*., 1991), as well as a megafauna that is more representative of reef-like structures. Indeed, the carbonate structures associated with methane seeps can increase the habitat complexity of the seabed, and as such may be inhabited by a variety of reef-associated biota, including fish (e.g. Burns *et al*., 2006), although it is questionable whether or not there is any increased abundance (Juhl and Taghon, 1993).

Various fish species are known to occur in such sites within the North Sea ecoregion, including hagfish *Myxine glutinosa*, cod *Gadus morhua,* haddock *Melanogrammus aeglefinus*, saithe *Pollachius virens,* four-bearded rockling *Enchelyopus cimbrius*, redfish *Sebastes* spp., long-rough dab *Hippoglossoides platessoides* (Dando *et al*., 1991; Jensen *et al*., 1992). In the Norwegian Sea, the fauna of the methane seeps associated with the Haekon Mosby mud volcano were described by Gebruk *et al*. (2003), who reported that the zoarcid fish *Lycodes squamiventer* was common in the habitat.

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7 Changes in abundance, migration and distributions patterns and sensitivity of marine ecosystems to climate variability and regime shifts

ToR f) Prepare review papers for the chapters of the ICES position paper on Climate Change on:

i) Changes in abundance, migration and distributions patterns;

ii) Sensitivity of marine ecosystems to climate variability and regime shifts

7.1 Introduction

Climate change processes and predictions of impacts is a key topic in the ICES Science Plan (Annex 7). To address this issue, the ICES Study Group on Climate Change (SGCC) met for the first time at ICES Headquarters, Copenhagen, Denmark in June 2008. Subsequently, SGCC produced an ICES brochure addressing oceanic climate change (ICES – Climate Change: Changing Oceans -

http://www.ices.dk/iceswork/bulletin/ICES%20CLIM.pdf) that drew on the previous work of WGFE (ICES 2008). For 2010, an ICES (white) position paper on climate change was cited as a key product of SGCC. In 2008, Daniel Duplisea, then Chair of WGFE presented a summary of the groups work on "Climate Change and Fish Communities" (ICES response to the OSPAR Request on Climate Change). The request for WGFE was to take the lead in the proposed chapter 9 and contribute to chapter 10, as explicated in the ToR provided to WGFE in 2008. Prior to this meeting of WGFE, a first draft for the two chapters constructed by the previous and present chairs of WGFE (Daniel Duplisea and Dave Kulka) has been circulated outside of WGFE. Following this circulation, various comments were received via email. The following sections constitute the contribution of WGFE to the position paper on climate change. Annex 8 summarizes the comments received and provides guidance for further work on the WGFE contribution to the climate change position paper chapters.

The e-mail comments have been incorporated where possible in both chapters. This has led to some changes, for example broadening the original theme for Chapter 9, the justification for these changes have been explained in section 7.4, following the two chapters. Because WGFE is to make a contribution to chapter 10, rather than creation of the entire chapter, our focus there has been limited to fish, while it is recognized that the ecosystem topic which it discusses is greater in scope. However, WGFE considers how it set up chapter 10 as a structure which other groups or experts can easily extend with the processes and examples other than those affecting fish.

Some discussion was directed to the goals of the position paper. In the first instance, the draft and the work seemed to be focussing on reviewing effects of climate change, but this did not seem to constitute an ICES position on climate change. To extend beyond the review, a section in each chapter is included which gives a focus for further research. That should contribute (according to the WGFE) to ICES' position on research around climate change.

7.2 Changes in abundance, migration and distributions patterns (Chapter 9, ICES Climtate Change Position Paper)

Warming is one of the most prominent features of the ongoing and predicted climate change. In the context of rising sea temperatures, it must be emphasized to consider that fish are poikilothermic organisms whose internal temperatures vary, often matching the ambient temperature of the immediate environment. A change in water temperature thus directly affects the internal temperature and consequently the physiological processes of the fish and consequently the behaviour. If the temperature is (too) low, physiological processes stop or proceed very slowly. When temperatures rise, internal processes accelerate until an optimum is reached, beyond which, processes slow down again and conditions eventually become lethal. This optimum curve is generally steeper beyond the optimum peak, indicating a smaller temperature range within which fish can survive above optimum temperatures than below their optimum temperature (e.g. temperature-growth curves, Fonds *et al*., 1992).

There is considerable variability of physiological tolerances and responses between species, within species (between populations) and among individuals within the same population. The individual can show an acute response or acclimatize to temperature, depending on degree and rapidity of temperature change, condition of the individual, as well other factors such as the level of available food and presence of other stressors. Acclimation can occur as a chronic response and adaptation measured in time-scales of generations, as an evolutionary response. Population level differences have been observed by Svåsand *et al.* (1996) who found significantly higher growth rates and lower condition factors for Norwegian coastal cod compared to Arcto-Norwegian cod when fish from both populations were reared within the same tank.

The overall temperature tolerance of fish species is one of the primary factors determining the differences in species distribution. Based on their affinity for specific temperature ranges and biogeographical distribution, species can be grouped, e.g. into Mediterranean, Lusitanian, Boreal, and Arctic species (Yang 1982, Engelhard *et al.*, subm.) which enables the correlation of climate change effects on the distribution of single species as well extrapolations to species groups with similar temperature and biogeographical preferences. Fish species that are be classified as "temperature keepers" (sensu Perry and Smith 1994) such as wolffish (Anarhichidae) (Kulka *et al.*, 2004) maintain a similar temperature range by changing their range or depth distribution. Under warming conditions it is likely that such species and groups will follow their preferred temperature, either entering new areas where temperature conditions have become suitable, or being forced out of areas where temperatures have risen outside their preferred limits. Examples for such distributional shifts are presented in the next section.

Similar to differences in thermal preferences between species, different life-stages of the same species often have different temperature requirements (Rijnsdorp *et al.*, 2009). These potentially limit the spreading of the species as the capability of different life stages in following preferred temperature ranges may be limited. Ocean currents, as well as temperature, are decisive in determining species distributions, and may also be altered by climate change (Corten 1990; Corten and Van de Kamp 1996). Eggs of some species require specific substrata (e.g. herring), salinities or currents to transport them into viable areas where larvae have food and/or juveniles can avoid predation or find suitable habitat. A change in currents or wind effects at the time of spawning or shortly thereafter may result in the loss of larvae to the population where they are transported to locations unsuitable for survival (Han and Kulka 2007). Thus, adults may move into new areas due to the rise in ambient temperature, but if conditions necessary for the survival of other life-stages are less than adequate, the species would not be able to reproduce successfully and therefore establish itself in the new area. Changes in currents that can be affected by changes in windfields, could, therefore, either further enhance a species distribution or limit their possibilities in areas already occupied.

Temperature change indirectly affects the availability of food in appropriate habitats of fish and may thereby limit the capability of fish to respond by a change in distribution. Some species distributions are confined to specific substrata (e.g. lesser weever *Echiichthys vipera* on sandbank crests in the North Sea, Ellis *et al.* in prep.) or structures (e. g. cold water reef fish, Northeast Atlantic, Costello *et al.* 2005). But they also need food to survive, which for example could limit their distribution into less structured habitats.

Also, salinity, especially in coastal areas and ice cover may be affected by warming. Altered precipitation changes freshwater inflow through river discharge or melting ice and can affect marine coastal species (e.g. feeding success of fish larvae, Fortier *et al.*, 1996). Ice cover can be a major influence in northern areas, where some species require ice cover for survival (larval survival for species such as polar cod, *Boreogadus saida,* Fortier *et al.*, 2006), while it limits many others species to extend into the areas covered by winter ice, although summer temperatures there may be suitably warm. The ice cover shows that even when average temperatures or conditions change, a short period of extreme conditions could limit the capability of species to survive or permanently inhabit the area. As well, long-term warming affects extent and duration of ice cover, potentially affecting fish species in a multitude of ways.

The climate predictions are that extreme events are likely to increase, e.g. extremely warm temperatures (heat waves) but also more storms and heavy rain fall events. A storm during larval dispersal could transport larvae to locations where chance of survival is low, while it is shown that a heat wave of short duration, two or three days is enough to seriously diminish the abundance of the stationary fish species eelpout, *Zoarces viviparus*, in the Wadden Sea (Pörtner and Knust, 2007).

Multiple, interactive aspects of climate change therefore can result in a bottleneck for changes in the distribution and survival of fish. Defining the specific timing and factors causing bottlenecks for the population growth and spatial spreading is crucial to predicting possible future population changes. These types of predictions have been performed using the 'bioclimatic envelope modelling' approach (Pearson and Dawson, 2003), where the envelope consists of the various environmental conditions within which a specific species can survive. By combining these envelopes with predicted physical changes in the environment, predictions of future species ranges can be made. A worldwide analysis has recently been carried out using this technique (Cheung *et al*., 2009). Based on 1066 commercial fish and invertebrate species, the study suggested that climate change could lead to numerous local extinction events by the year 2050, especially in subpolar regions, the tropics and semi-enclosed seas (e.g. the Mediterranean), with pelagic species (such as herring and anchovy) distributions moving pole-wards by up to 600 km and demersal species (such as cod and haddock) by an average of 223 km.

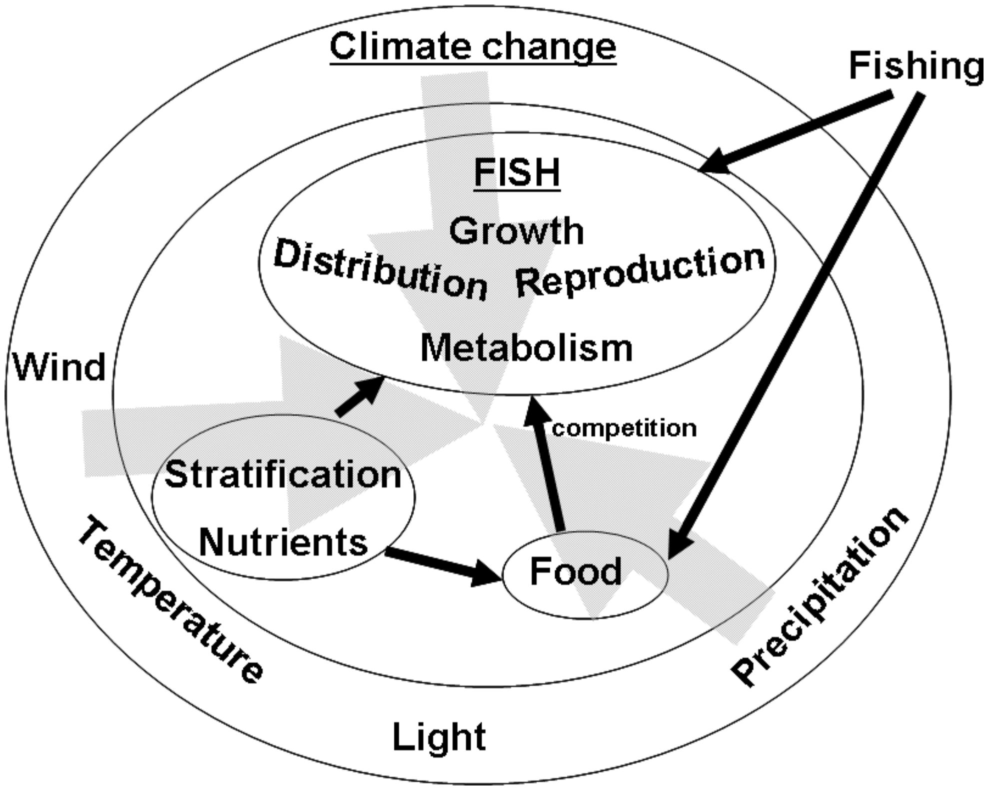

Figure 7.1. Schematic representation of climatic drivers affecting fish populations in a direct or indirect manner. The outer circle represents the climatic drivers, which affect (the grey arrows) most aspects of the ecosystem (the inner circles). The three inner circles are biotic factors (food and fish) and abiotic factors (stratification and nutrients). The black arrows represent the impact from fishing (or other anthropogenic effects), abiotic factors and food on fish (shown with the possible mechanisms affected).

7.2.1 Temperature induced changes in abundance, distribution and migration patterns

A large proportion of literature addressing effects of climate change on fish populations stems from correlative studies between time-series data on single species or stocks and climate variables. Such statistical analysis has revealed changes in the abundance and distribution of fish species that correlate well with environmental variables. Climate related changes in the distribution of marine fish are thus well-documented for numerous species and across a number of regions (e.g. *Arctic - the Nordic Seas)*: Astthorsson *et al.*, 2007, Berge *et al.*, 2005, Bjoernsson and Palsson 2004, Drinkwater, 2009, Toresen and Østvedt, 2000; *North Sea*: Beare *et al.* 2004, Brander *et al.* 2003, Dulvy *et al.*, 2008, Perry *et al.*, 2005, Rindorf and Lewy 2006; *Celtic Seas*: Cotton *et al.*, 2005, Houghton *et al.*, 2006, ICES, 2007, Sims *et al.*, 2003; *Bay of Biscay and Iberian Coast*: Bañón and Sande, 2008, Sánchez and Serrano, 2003; *Baltic Sea*: Aro and Plikshs, 2004, Nielsen *et al.*, 1998; *Barents Sea*: Drinkwater *et al.*, 2006; see also Figure 7.2 and Table 7.1).

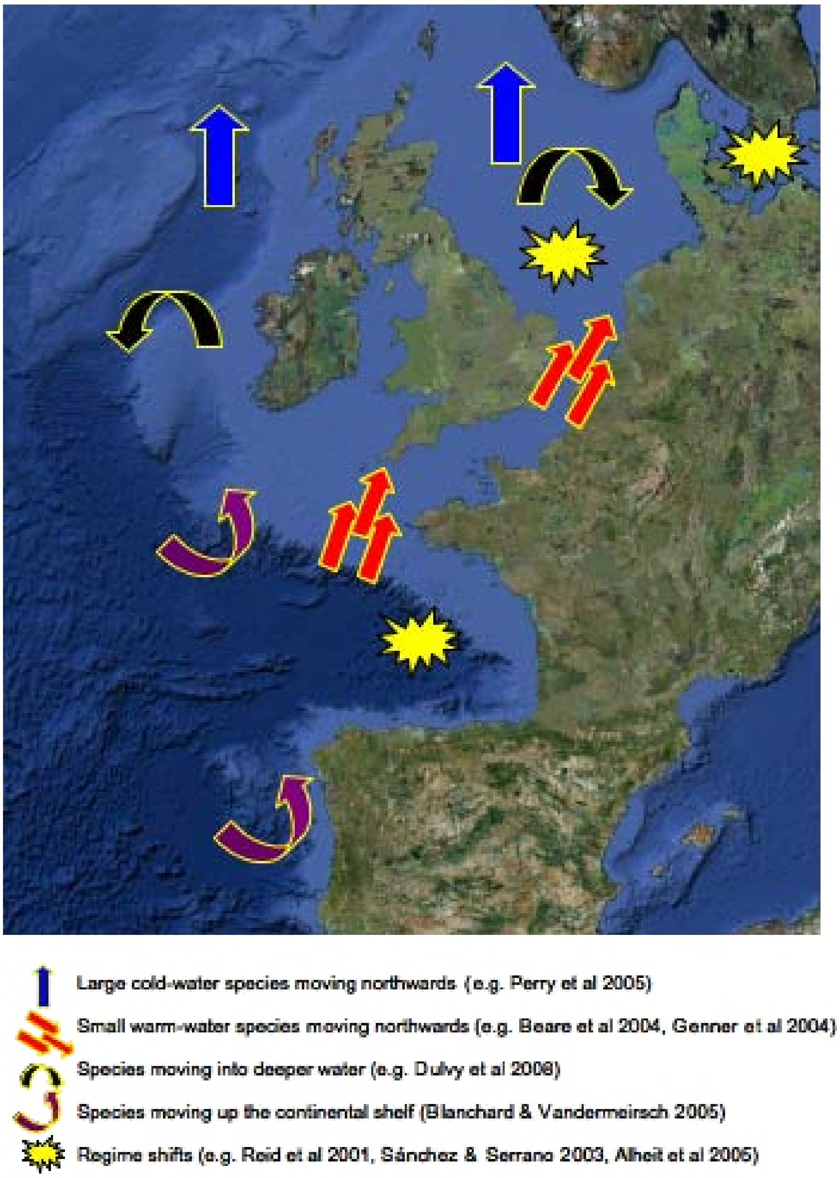

Figure 7.2. Reported climate-induced changes in species distributions and assemblage composition.

Shifts in distribution are generally most evident near the northern or southern boundaries of a species range, where theoretically, warming results in a distributional shift northward, and cooling draws species southwards for both warm- and cold-water species (Rose 2005). The warming trend in the Northeast Atlantic, for example, has coincided with a northward shift in the distribution of fish species from southerly latitudes (Beaugrand *et al.*, 2002, Beare *et al.*, 2004, Perry *et al.*, 2005, Quero *et al.*, 1998, ICES, 2008), but examples for such shifts in distribution can be found consistently across regions (e.g. *Arctic waters*: Astthorsson and Palsson, 2006, Astthorsson *et al.*, 2007, Bjoersnsson and Palsson, 2004; *Celtic Sea*: Stebbing *et al.*, 2002; *Bay of Biscay and Iberian Coast*: Quero *et al.*, 1998).

The latitudinal response to warming in the North Sea demersal fish assemblage is heterogeneous and due to a composite of at least two patterns: (i) a northward shift in the average latitude of abundant, widespread thermal specialists (grey gurnard and poor cod), and (ii) the southward shift of relatively small, southerly species with limited occupancy and a northern range boundary in the North Sea (scaldfish, solenette, bib, sole and lesser-spotted dogfish, Dulvy *et al.*, 2008). The southward shift of warm-tolerant Lusitanian species is consistent with climate change acting: (i) through the warming and increasing availability of shallow habitats in the southern North Sea, and (ii) through North Atlantic Oscillation-linked inflows of warm water into the NE North Sea. The availability of shallow habitats can be temporary, as a single cold winter may force species to vacate the area (e.g. solenette and scaldfish, Van Hal *et al.*, 2009), resulting in the need for remigration and recolonization into the areas.

The distribution of temperature from shallow to deep water is similar to the north–south distribution of temperature. Therefore, in addition to latitudinal shifts, a shift to deeper water is likely. This is shown for the North Sea demersal fish assemblage which has deepened by ~ 3.6 m decade^{-1} in response to climate change (Dulvy *et al.*, 2008, Van Keeken *et al.*, 2007), a finding that was coherent for most assemblages under study. Thus, although mean latitude shows no change for some species, a response to climate maybe found instead as shift to deeper, cooler depths, e.g. plaice (Perry *et al.*, 2005; Van Keeken *et al.*, 2007), and cuckoo ray (*Leucoraja naevus*, Perry *et al.*, 2005). Hedger *et al.* (2004) showed that cod were found in deeper water during 1990–1999 compared to 1980–1989, but their distribution with respect to temperature was unchanged. A similar large-scale shift to deeper waters was observed in the Northwest Atlantic (off Newfoundland and Labrador) due to thermal changes except the response was to a period of cooling. The species moved to deeper, warmer waters in this case (Atkinson, 1994).

Distributional shifts can result in the appearance and increase in abundance of rarer migrant species to a particular area. An example is the current influx of snake pipefish (*Entelurus aequoreus*) to the North Sea (Harris *et al.*, 2007, Kloppmann and Ulleweit 2007, Lindley *et al.*, 2006, van Damme and Couperus 2006), which is hypothesized to either, (i) coincide with a rise in winter, spring and summer sea temperatures (January–September), when the eggs are developing and the larvae are growing in the plankton (Kirby *et al.*, 2006), or (ii) result from changes in zooplankton (prey) availability which in turn has been caused by changes in the hydroclimatic environment (van Damme and Couperus 2006). In the Celtic Sea, an increase in sightings of rare migrant species, such as bluefin tuna (*Thunnus thynnus*), triggerfish (*Balistes capriscus*), thresher (*Alopias vulpinus*), blue sharks (*Prionace glauca*), sting-rays (Stebbing *et al.*, 2002), ocean sunfish (*Mola mola*, Houghton *et al.*, 2006) and sailfin dory (*Zenopsis conchifer*, Swaby and Potts 1999) have been reported. Similarly, new records of tropical affinity species have increased in the Bay of Biscay and along the Iberian Coast (Arronte *et al.*, 2004, Bañón 2000, 2004, Bañón and Sande 2008, Bañón *et al.*, 2002, 2006, 2008, Punzón and Serrano 1998). Two species related to this phenomenon were the grey triggerfish (*Balistes carolinensis*) and the flatfish (*Solea senegalensis*), previously unknown but now showing a relevant biomass (Bañón *et al.*, 2002). In most of the cited papers, climate change is described as the driving agent of this increase (ocean warming and/or changes in current patterns in the North Atlantic bringing more southerly water into the northeast), however the increased exploration of deep-sea fish resources in recent years that has enhanced the discovery of new deep-water species northward of their known distribution area must be considered (Bañón *et al.*, 2002).

Changes in distributions of fish species can also be observed as range extensions/retractions and coincide with an increase/decrease in overall abundance (Table 7.1, see also Chapter 5 of this report) as ranges expand/retract and new areas become occupied/vacated. For example, in northern waters, the abundance of Norwegian spring-spawning herring has risen since the temperature increases in the 1990s (Toresen and Østvedt, 2000) and the population now migrates out into the Norwegian and Greenland Seas toward Iceland to feed and spawn (ACIA 2005), whilst capelin, whiting, blue whiting, haddock and anglerfish show a similar large increase in abundance as well as distribution extensions (Berge *et al.*, 2005, Astthorsson *et al.*, 2007). An increase in abundance of southern species in the North Sea, anchovy (*Engraulis encrasicolus*), striped red mullet (*Mullus surmuletus*), pilchard (*Sardina pilchardus*), John Dory (*Zeus faber*) and snake pipefish (*Entelurus aequoreus*), (Beare *et al.*, 2005) has been related to an increase in flow of Atlantic water through the straits of Dover coupled with favourable winter conditions (Corten and van der Kamp 1996, ICES, 2008). Fluctuations in relative abundance of basking sharks within the Celtic Sea area have been positively correlated with fluctuations in SST and the NAO (Cotton *et al.*, 2005) and although prey density is a key factor determining short term distribution patterns (Sims and Quayle, 1998), long-term behavioural choices by basking sharks may relate more closely to occupation of an optimal thermal habitat that act to reduce metabolic costs and enhance net energy gain (Crawshaw and O'Connor 1997, Sims *et al.*, 2003).

Whilst species habitat occupancy, latitudinal, and depth distributions appear to be changing in response to interannual variation in several measures of temperature and/or hydrography, there is no single biogeographical measure that consistently responds to a single measure of temperature or hydrography across the range of species. Instead, considerable heterogeneity is found in individual species' response to the various measures of climate variability, and there remains scope to determine the underlying ecological factors, such as niche (pelagic/demersal), trophic level and particularly body size.

Comparative studies highlight a substantial proportion of species that do not appear to change distribution in response to climate variability (within the range of variability observed over the last fifty years). The analysis presented in ICES (2007, 2008) seems typical of multispecies climate-biological response analyses, where species show heterogeneous responses and as a consequence it can be difficult to uncover general patterns. Due to the species-specific responses to climate-change, classifying species into sets of 'ecotypes', based on similarities in certain relevant biological characteristics (biogeographical affinity, reproductive mode, body size, trophic niche and habitat), may facilitate extrapolations from one species to others and thus allow for predictions of the potential effects of climate change on fish assemblages. Perry *et al.* (2005) found it difficult to define a single relationship between life histories and distributional response and based their conclusion on a categorical test (large vs. small) rather than treating body size as a continuous variable. It may be that the variance in individual species trends confounds efforts to uncover a general pattern. The focus of climate-fish studies is thus developing toward an ecosystem-scale indicator of the biotic response of the aggregate demersal fish assemblage to climate variability and longer term climate change (Dulvy *et al.*, 2008).

Table 7.1. Summary of observed changes in mean abundance (mean number per tow) in a) Barents Sea, b) North Sea, c) West of Scotland and Celtic Sea, and d) Bay of Biscay between the periods 1977–1989 vs. 2000–2005 and 1990–1999 vs. 2000–2005 (for given Quarters). The mean catch per species was calculated by averaging the mean catches per subarea (either depth range or ICES-rectangle, depending on the stratification of the survey) for the entire period. The change in abundance was determined by the difference between the means of two periods, categorized by 'no change' (o), a small increase or decrease of 10–50% (+ or -), a medium change of 50–100% (++ or --), and a large change of more than 100% (+++ or ---). Table adapted from WGFE report, (ICES 2008).

a) Barents Sea

		1977–1989 vs. 2000–2005	1990–1999vs. 2000–2005	1990–1999 vs. 2000–2005
	Quarter:	**3**	**3**	NA
Species				
Squalus acanthias	spurdog	- -	+++	NA
Amblyraja radiata	starry ray	+++	-	NA
Raja clavata	thornback	- -	- -	NA
Gadus morhua	cod	+	- -	NA
Melanogrammus aegle-	haddock	+++	o	NA
Merlangius merlangus	whiting	-	o	NA
Lophius piscatorius	anglerfish	- -	-	NA
Pleuronectes platessa	plaice	++	- -	NA
Pollachius virens	saithe	- -	+++	NA
Clupea harengus	herring	o	+++	NA

b) North Sea

		1977–1989vs. 2000–2005	**1990–1999 vs. 2000–2005**	**1990–1999 vs. 2000–2005**
	Quarter:	**1**	**1**	**3**
Species				
Northern North Sea				
Raja clavata	thornback ray	- -	- -	- -
Merlangius merlangus	whiting	- -	-	- -
Merluccius merluccius	hake	++	+	+
Pleuronectes platessa	plaice	+++	+	++
Sardina pilchardus	pilchard	+++	+++	+++
Pollachius virens	saithe	+++	+++	+++
Zeus faber	john dory	+++	+++	+++
Mullus surmuletus	striped red mullet	+++	+++	+++
Southern North Sea				
Scyliorhinus canicula	lesser spotted dogfish	+++	+++	+
Squalus acanthias	spurdog	- -	- -	- -
Sprattus sprattus	sprat	++	+	+
Engraulis encrasicolus	anchovy	+	+++	+++

		1977–1989vs. 2000–2005	**1990–1999 vs. 2000–2005**	**1990–1999 vs. 2000–2005**
Melanogrammus aeglefinus	haddock	+++	+++	++
Solea vulgaris	sole	- -	-	-
Sullus surmuletus	striped red	+++	++	O

c) West of Scotland (WS) and Celtic Sea (CS)

		1977–1989 vs. 2000–2005	**1990–1999 vs. 2000–2005**	**1990–1999 vs. 2000–2005**
	Quarter	**1 *(WS)***	**1 (WS)**	**4 (CS)**
Species				
Sprattus sprattus	sprat	+	+++	+++
Engraulis encrasicolus	anchovy	+++	+++	+++
Sardina pilchardus	pilchard	+++	+++	+++
Helicolenus dactylopterus	blue-mouth	+++	+++	+++

d) Bay of Biscay

		1977–1989vs. 2000–2005	**1990–1999vs. 2000–2005**	**1990–1999 vs. 2000–2005**
	Quarter	*NA*	**4**	*NA*
Species				
Sprattus sprattus	sprat	*NA*	+++	*NA*
Engraulis encrasicolus	anchovy	*NA*	-	*NA*
Helicolenus dactylopterus	blue-mouth	*NA*	+++	*NA*
Sardina pilchardus	pilchard	*NA*	++	*NA*
Zeus faber	john dory	*NA*	+	*NA*
Capros aper	boarfish	*NA*	-	*NA*

NB: Increase/decrease = +++/--- >100%; ++/-- 50–100%; +/- 10–50%; o = no change.

7.2.2 Climate-induced changes in the growth, maturation and recruitment of fish

In addition to survival and distribution of fish, growth, maturation and reproduction are affected by changes in water temperature. These processes will determine the success of a species in terms of its population growth and abundance (e.g. Rijnsdorp *et al.*, 2009**)**.

Laboratory experiments have demonstrated optimum growth curves for each life stage - egg, larvae, juveniles and adults - under *ad lib* food conditions, meaning that increasing temperatures will result in increased growth (and development) until a certain optimum temperature after which growth decreases again (Fonds and Saksena, 1977). In the field, species do not live at their optimum temperature the whole year-round or have *ad lib* food conditions everywhere, which leads to differences in local growth-rates.

Favourable conditions prior to spawning can lead to higher egg production and earlier spawning. For example, earlier spawning periods have been shown to occur for both Plaice and Sole in relation to increasing sea temperatures in the North Sea, leading to an increased length of growing season for juveniles of both species and ultimately resulting in an increase in length of the 0-group by the end of the year (Teal *et* *al.*, 2008). However, at some point, increasing temperatures would become detrimental to the reproductive process.

Recruitment is determined by the quantity of eggs spawned and the conditions during hatching, and larval and juvenile development. Time to hatching and development vary under different temperatures, while survival of the prerecruits is determined by transport success (to settling locations, more, or less optimal for survival), which includes the availability of food, presence of predators as well as physical conditions such as depth and temperature.

The effect of increased temperature on different processes can combine forces and have a positive effect on the species population, while the processes can also counteract each other or result in a negative effect. For example, temperature rise may increase growth-rate but also decrease survival of eggs or larvae resulting in lower recruitment. Temperature is not the only factor influencing these processes. The availability of food will determine growth-rate, and limited availability of food will reduce growth-rates. The availability of food is determined by the amount of nutrients and light but also by the amount of competitors for the same food source. Because food is affected by other factors than are the fish, changes in timing of reproduction or migration could result in a mismatch between when the fish need their food and the food is available: the match–mismatch hypothesis (Cushing 1974 1975, 1990, Durant *et al.*, 2005). An increase in temperature could advance the timing of reproduction. However, timing of algal growth is controlled more by light then by temperature and therefore timing of food production may not be advanced. This could result in a mismatch leading to starvation of the larvae. Thus, while temperature may improve development of the fish in certain cases, there ultimately may be a negative effect on the population due to failure of recruitment. The processes are indeed complex and highly interactive and thus predicting resultant affects due to climate change is very difficult.

7.2.3 Interactive effects of climate and fisheries

While climate variability and change evidently have an impact on marine fish populations, fish communities are also under intense pressure by fisheries. Distributional changes of fish in relation to climate, for example, are often exacerbated or confounded by fishing pressure and related mortality. Apparent temperature-related shifts in species distribution may, at least in part, be a consequence of local patterns of fishing pressure (Hutchinson *et al.*, 2001; Daan *et al.*, 2005; Wright *et al.*, 2006) leading to different rates of depletion in spatially segregated substocks (Hutchinson *et al.* 2001; Wright *et al.*, 2006). Synergistic effects of the two drivers, as well as counteracting processes, thus need to be addressed and investigated further. The response of fish stocks to climate should be considered in conjunction with the effects of fishing, with potential additive effects and feedback loops being investigated (Lehodey *et al.*, 2006).

Effects of fishing on fish populations are well-studied and are known to lead to broad-scale changes in abundance and distribution of fish stocks (see above) as well as changes in life-history parameters (e.g. Grift *et al.*, 2003, Jorgensen *et al.*, 2007, Hidalgo *et al.*, 2009). Furthermore, the intense pressure of fisheries on fish stocks is known to cause changes in fish community assemblages (i.e. loss of diversity, Smith *et al.*, 1991; Bianchi *et al.*, 2000; Jackson and Mandrak, 2002; Worm *et al.*, 2006, change in size-structure, Bianchi *et al.*, 2000; Dulvy *et al.*, 2004; Rochet *et al.*, 2003; Shin and Cury 2004; Daan *et al.*, 2005), which can have further implications for the ecosystem (e.g. trophic cascades, Daskalov *et al.*, 2007, Frank *et al.*, 2005, Möllmann *et al.*, 2008, Worm and Myers, 2003). Although these effects are well-known, the question remains as to how the observed changes in fish life-history, distribution, diversity loss and habitat modification (or loss) may alter the population's response to a changing climate. An example of synergistic effects of climate and fishing is shown for cod, where the fisheries induced change in spawning stock structure (decrease in age and length of average spawner, as well as number of age classes contributing to the spawning stock), is shown to strengthening the climate-cod recruitment link (Ottersen *et al*., 2006).

This leads to the question - how do fisheries induced changes in fish populations affect their ability to respond to climate variability and change, i.e. to buffer against poor year classes or the possibility of an evolutionary response to climate change? Synergistic effects of multiple drivers on fish populations, as well as counteracting processes thus need to be addressed and investigated further. Predicting the future effects of fishing and climate change, and the interactions between the two drivers, is a key challenge for future research (Greene and Pershing 2007). Part of this challenge will be to develop ecosystem models capable of representing the effects of multiple drivers on the fish community. Examples of current work in this direction include the large EU project MEECE (www. meece.eu; Travers *et al*., 2009a, b) which aims to use predictive models to explore the impacts of anthropogenic and climatic drivers on ecosystems, and the QuestFish project (http://web.pml.ac.uk/quest-fish/), which focuses on the potential impacts of climate change on future fisheries' productivity.

7.2.4 Future research directions

Effects of climate variability and climate change on fish populations are increasingly being documented using time-series analysis and a link undoubtedly exists. However, there are still many open questions on underlying mechanisms and processes, species resilience and adaptations to change. Therefore, future research should address:

- Disentangling climate variability (cyclic events) from climate change.
- Physiological processes underlying climate-fish relations to gain a better understanding of the mechanisms by which climate variability affects fish populations.
- Differences in vulnerability of the different life-stages of fish (eggs, larvae, juveniles, adults), identifying where potential bottlenecks may arise.
- The (dis)similarity in species responses, i.e. response of northern vs. southern species, pelagic vs. benthic species, deep-sea vs. coastal shelf species, r- vs. k-strategists, specialist vs. generalizts, etc. and potential grouping of species into categories which may be similarly affected by climate change.
- The interaction between climate change and fisheries effects on fish populations, including effects of fisheries on species resilience and the ability to adapt to climate change through selective fishing effects on species genetics.
- Effects of climate change on fisheries through effects on fish growth, maturation, recruitment, survival etc.
- Modelling techniques for synergistic top–down (fisheries) and bottom-up (climate) effects. Different types of models will be required to look at different aspects; for example, a proper representation of bioenergetics will be required for exploring the impact of climate on fish physiology, while tially resolved models will be required to look at distributional changes.

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7.3 Sensitivity of marine ecosystems to climate variability and regime shifts (Chapter 10, ICES Climate Change Position Paper)

7.3.1 A. Sensitivity of marine ecosystems to climate variability

7.3.1.1 Effects of climate variability on marine ecosystems

The marine environment is a complex system that varies over different temporal scales, ranging from predictable daily (light, tides) and seasonal (freezing, stratification) patterns, through short-term unpredictable (storms) and longer term cyclical (El Niño and NAO) events, to potentially long-term directional changes (warming, ice ages).

In the last few decades, including in the Northeast Atlantic, natural patterns of variation have been occurring in tandem or in interaction with a potentially longer term trend of prolonged warming. This change in the climate is predicted to influence the marine environment through several processes. While it must be emphasized to investigate and experimentally examine the effect of each process in isolation, it must be emphasized to keep in mind that many of the processes are closely coupled, or are even causally related. Multi-process couplings can be either predictable or seemingly chaotic in nature and may include non-linear and tipping-point relationships.

Water temperature is a key determinant in species distributions. Past evidence and future predictions suggest a warming trend over the next century (e.g. Sheppard 2004). In terms of the impact of temperature on marine ecosystems, it is not necessarily the annual means that have the highest influence. Rather, for Lusitanian species, winter minimum temperatures may determine northern limits, while for Boreal species; summer maximum temperatures may determine the southern limits of their distributions. Furthermore, winter or summer means may determine reproductive timing and success and larval survival, and in combination contribute to the strength of recruitment pulses.

Particularly in shallower zones such as the southern North Sea, bottom temperatures are in part determined by the level of mixing in the water column, which in turn can be limited by seasonal thermoclines. Thermoclines are a result of summer warming of surface layers affecting water density, and can present a hydrographical barrier to nutrient transport, thus limiting summer primary production. Climate change may cause increased wind strength and durations and storms (Hulme *et al.,* 2002), which could in turn compromise the prevalence of summer thermocline. Nutrients for primary production may also enter shallow seas through upwelling of deeper water, which is also influenced by wind strength and conditions. The tension between surface water warming and thermoclines with wind-forced mixing and upwellings makes predicting nutrient availability a complex undertaking.

Patterns of precipitation are seasonally variable, but predictions are for an increase in precipitation in northern Europe and a decrease in southern Europe, which will have knock-on effects on run-off and the delivery of riverine nutrients to shallow seas. For example, run-off is expected to increase nutrient loadings in the Bay of Biscay, but reduce nutrient transport to the Mediterranean, leading to contrasting patterns in the production of sole (Salen-Pickard *et al.,* 2002, Le Pape *et al.,* 2003, Darnaude *et al.,* 2004).

Finally, the physical chemistry of seawater is highly dynamic, with freshwater run-off and atmosphere-seawater interactions causing predictable and stochastic, short-term and instantaneous chemical heterogeneity. Climate change is expected to change seawater chemistry in terms of changes in salinity, particularly due to changes in patterns of ice formation and melting, and due to the uptake of anthropogenic carbon dioxide from the atmosphere and the resulting formation of carbonic acid causing a decrease in seawater pH (see discussion of potential affects at the physiological level below).

7.3.1.2 What are the observed and predicted effects of climate variability?

The effects of climate variability on marine ecosystems are the result of changes in the dynamics and distributions of populations and assemblages that are determined by growth, survival and behaviour of individuals. All of these processes are underpinned by the sum of the instantaneous effects of the proximate environment on physiological processes within each individual within the assemblage (see Rijnsdorp *et al.* 2009 for a recent review).

At the physiological level, temperature has a direct effect on metabolic costs and scope, which has knock on effects on activity, growth, and reproduction. The influence of the environment often changes in magnitude with ontogeny. For example, eggs and larval stages exhibit narrower thermal tolerances due to their high metabolic rate and low energy reserves. Coupled with the inability of early life stages to move to preferred or optimal locations/conditions, this can have a significant affect of survival of the early stages. Temperature can also effect the rate and timing of egg maturation and spawning, with phenological knock-on impacts on the match–mismatch of larval stages and their plankton prey. Recent work has indicated that ocean acidification caused by increasing anthropogenic CO_2 in the atmosphere (linked to climate change) may not only affect taxa that build skeletons, shells or tests (Guinotte and Fabry, 2008) but also fish, impacting on egg fertilization and the early survival of larvae. Ishimatsu *et al.* (2005) for example, indicated that CO_2 enriched seawater can be toxic to eggs and larvae of fish.

At the organism level, the effects of climate variability and climate change can manifest in terms of day-to-day behavioural and activity patterns, movement decisions (during dispersal and in later life), and ultimately by influencing the likelihood of life cycle closure, growth, reproductive output, and longevity. In terms of the influence of temperature, there is mounting evidence that species distributions have responded to recent patterns of climate change. For example, some boreal species are moving poleward (Perry *et al.*, 2005). This movement can be driven by northward forcing of larval stages coupled with elevated larval survival (Rindorf and Lewy, 2006) rather than movement of adult fish that may fail to optimize their temperature regime even if small-scale movement would lead to more favourable conditions (Neat and Righton 2007). In parallel with northward shifts in distributions, many species in the Northeast Atlantic are also responding to warming by moving to deeper (cooler) water conditions (Dulvy *et al.* 2008). The effects of temperature may also influence the phenology of movement of fish to annual spawning and feeding grounds (Carscadden *et al.*, 1997, Sims *et al.*, 2004).

At the population level, climate variability and change can influence the balance of mortality, growth and reproduction, and alter dispersal patterns. This effect can have an impact on the ability of larvae to settle, later-stage fish to locate to new areas with more favourable conditions and can force populations to leave traditional sites. Since early life stages are more sensitive at both the physiological (metabolizm) and organismal (survival, dispersal) level, the additive effects of climate variability may lead to changes in larval growth and mortality which can effect recruitment success (Houde, 1987). Changes in the match–mismatch of larvae to their planktonic prey and the likelihood of connectivity between spawning and nursery areas may also combine to exert novel bottlenecks that affect population size and productivity, ultimately altering the realized distribution and abundance of fish. Finally, increased temperature and thus elevated growth-rates may alter the age and size at maturity, usually resulting in earlier and smaller maturing fish. This earlier bias towards reproductive allocation compromises adult growth (Heino *et al.*, 2002) and thus the biomass productivity of a harvestable population.

At the ecosystem level, climate variability and change can influence the timing and magnitude of nutrient supply (see Section 7.3.1.1), which in turn will affect primary and secondary productivity, and ultimately determine the productivity of the ecosystem, including the harvestable component. For example, increased winds may cause upwelling and this can lead to increased primary and fish productivity and change the timing of stratification. In turn, this can alter the phenology of spring plankton blooms. As well, changes in precipitation associated with climate change may alter the supply of terrestrial nutrients. Changes in the match–mismatch dynamics of larval fish with their prey (Cushing 1990) have already been seen in the breakdown of phenological coupling of cod larvae with plankton in the North Sea (Beaugrand *et al.*, 2003).

Ecosystems are highly complex and the result of many direct and indirect trophic and competitive interactions and/or changes in productivity caused by climate variability/change can permeate throughout the system, altering the balance of intra- and interspecific competition and predator-prey relationships. Changes may be subtle and/or gradual, but may also create tipping-points which can lead to regime shifts (see Section 7.4). Changes in the relative abundances of species within assemblages will result from the latitudinal redistribution of species ranges (Cheung *et al.*, 2009; Perry *et al.*, 2005) and the movement of some species to deeper water (Dulvy *et al.*, 2008) combined with the movement of deeper-water species into shelf seas (Blanchard and Vandermeirsch, 2005; ICES, 2008; Petigas *et al.*, 2009).

7.3.1.3 What do we still need to know?

In terms of the response of marine ecosystems to climate variability/change, some key questions remain. In addition to adaptation to change by range and depth shifts, many populations will show adaptation by phenological changes to key life-history processes (e.g. spawning, migrations), changes in dietary and habitat preferences in response to local conditions and changes in demographic characteristics (e.g. growth, age at maturity). The extent to which these changes can occur over the time frame imposed by contemporary and predicted trends will vary between populations and species. Likely predictors of sensitivity or resilience to change and measures of the realized rate of adaptability are important areas for future research. Key parameters to investigate include:

- the influence of ecosystem complexity, including the importance of functional redundancy which leads to many weak readily interchangeable links
- sensitivity of populations to winter and summer temperature extremes which would increase with climate change
- the influence of dietary preferences (narrow vs. broad) on sensitivity
- the influence of habitat preferences (pelagic vs. demersal) on sensitivity
- the balance between fixed genetic factors vs. phenotypically plastic responses

- life-history characteristics that lead to elevated sensitivities (fecundity, generation times), including the difference in response by r- and K-strategists
- the influence of dispersal capabilities on sensitivity
- the adaptability of socially and culturally mediated behaviours such as migrations

Finally, three fundamentally important questions to address are:

- To what extent are recent patterns of population, species, assemblage, and ecosystem change due to multidecadal cycles vs. climate change?
- Is ecosystem change gradual or can it be abrupt, resulting in regime shifts (Sect. 7.3.2), and is it uni- or bi-directional
- How does climate variability and change interact with other potential drivers (e.g. fishing) to bring about the observed patterns of ecosystem change?

7.3.2 Regime shifts in marine ecosystems

7.3.2.1 Regime shifts

Climate change impacts have been observed on individual species and species subsets. However, it is not clear if there are observable systematic and coherent assemblage-wide responses to climate change that could be used as representative indicators of changing state. Prediction of ecological regime shifts is notoriously difficult (Biggs *et al.*, 2009) and even what constitutes a regime shift is not clear (refer to description below). Further, the question of whether or not climate change can cause a regime shift is a topic of considerable interest given the potential affects on ocean state and fisheries systems (Scheffer *et al.*, 2001; Rothschild and Shannon, 2004).

Gradual changes in the environment generally result in gradual changes in the ecosystem. However, studies have shown that not only drastic change can result in contrasting ecosystem state (Scheffer *et al.*, 2001) but even in the absence of dramatic external changes, shifts to contrasting state have been observed (Scheffer and van Nes 2004). According to Collie *et al.* (2004) "the shift between ecosystem states can be caused by gradual, cumulative changes in the forcing variable(s) or it can be triggered by acute disturbances, either anthropogenic or natural". The change to a contrasting state is sometimes referred to as a regime shift. The definition of a regime shift is a rapid reorganization of the climate system or of ecosystems from one relatively stable state to another (Rodinov 2009, http://climatelogic.com/stars.html). Often, systems are relatively inert over a range of conditions but respond more strongly when key parameters reach certain threshold values. The most dramatic effects occur if the system has more than one attractor, so that it can be in alternative regimes at the same external condition. This has three important implications, which can be understood intuitively from graphs of stability landscapes (Scheffer and van Nes, 2004) Figure 7.3:

- Catastrophic transitions: Dramatic regime shifts occurring in response to small change in an external condition.
- Hysteresis: The phenomenon that catastrophic shifts are not reversible by an equally small reverse change in the external condition.

- Changing resilience: The size of the attraction basin (resilience) changes with external conditions, implying changes in 'brittleness', i.e. the likelihood of a stochastic event triggering a regime shift.

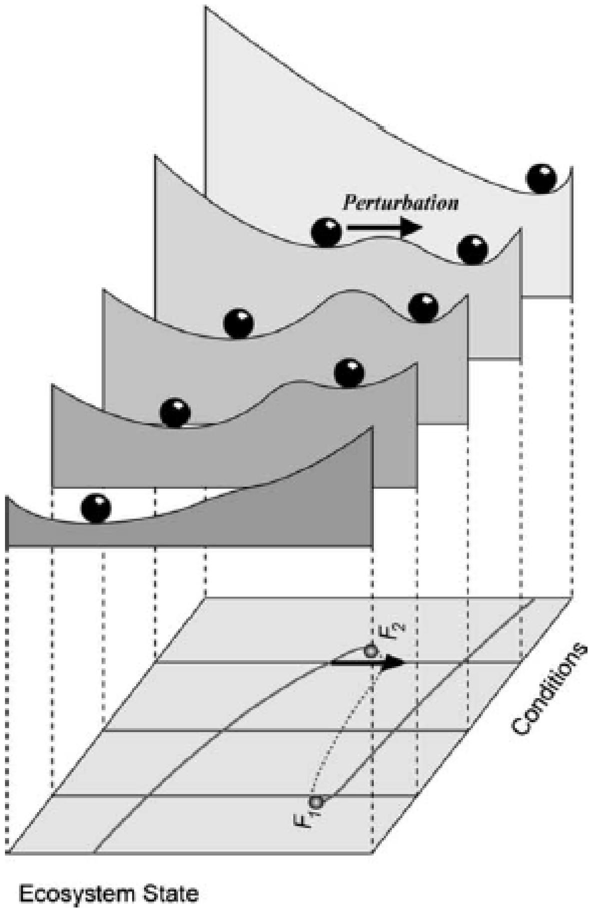

Figure 7.3. Implications of alternative stable states (as depicted in (a) of Figure 7.1) illustrated by stability landscapes. Each landscape represents the basins of attraction (valleys) that exist at a certain external forcing condition (e.g. temperature or exploitation pressure). When the ecosystem is in a state on the upper branch of the folded curve and conditions change sufficiently to pass the threshold (Saddle-node or fold bifurcation F_2) a catastrophic transition to the lower branch occurs. In order to induce a switch back to the upper branch, it is not sufficient to restore the environmental conditions before the collapse (F_2). Instead, one needs to go back beyond the other bifurcation point (F_1), where the system recovers by shifting back to the upper branch. If there are alternative stable states, a sufficiently severe perturbation may also bring the system into the basin of attraction of another state. This happens more easily if the basin of attraction (the resilience) is small (Scheffer *et al.*, 2001).

Defining a regime shift in terms of physical environmental variables is difficult but not impossible. For climate indicators such as the North Atlantic Oscillation (Reid *et al.*, 2001, Alheit *et al.*, 2005) or various physical indices for the North Pacific such as the Pacific Decadal Oscillation (Hare and Mantua 2000), sharp transitions have been observed in the past (Alley *et al.*, 2003).

Determining shifts in biotic aspects of the ecosystem is more challenging. Regime shifts in marine plankton systems have been proposed or inferred (e.g. Alheit *et al.*, 2005; Alheit 2009; Beaugrand 2004; Daskalov *et al.*, 2007; Hare and Mantua 2000; Scheffer and Carpenter 2003; Reid *et al.*, 2001; Weijerman *et al.*, 2005). However, whether these reported changes constitute regime shifts (abrupt, persistent changes, constituting a fundamental reorganization of community structure) remains unclear. Regime shifts in demersal communities are discussed under Section 7.3.2.2.

Various mathematical and statistical tools have been developed for detecting regime shifts, such as non-linear regression (e.g. Litzow 2006) or sequential t-test analysis (e.g. Rodionov *et al.*, 2004), that detect the possibility of a regime shift in real time. At the ecosystem level, the existence of and likely detection of a regime shift usually depends on all aspects of the system changing at the same time. Due to individual biological response times, it is unlikely that all components of the ecosystem change at the same time, rather it is expected that specific aspects change with a time-lag, complicating the detection of the shift.

The next step would be to detect the possibility of a shift before it happens, employing early-warning signals. It is suggested to use the speed of recovering after minor perturbations. For eight ancient abrupt climate shifts (Dakos *et al.*, 2008), it has been shown that they were all preceded by a characteristic slowing of the fluctuations well before the actual shift. Nevertheless, in order to predict ecosystem response to climate change, knowledge of their level of resilience is a prerequisite (Nyström 2000; Hughes 2003; Folke *et al.*, 2004; Walker *et al.*, 2004).

7.3.2.2 Climate change within the ICES area – Comparison of systems, case study

One of the earliest reported regimes shifts in terms of demersal communities occurred in the Gulf of Alaska (North Pacific), where a system previously dominated by shrimp and forage fish changed to one comprising large piscivorous fish in 1976–77, corresponding to a shift to a positive state of the Pacific Decadal Oscillation (PDO) (Anderson and Piatt, 1999; Mueter and Norcross 2000). In spite of a return of the PDO to a negative state in 1998–1999, there was no accompanying shift or return to the former state in the community structure (Litzow, 2006).

Similarly, there was an abrupt shift in the demersal community of the northeast Newfoundland and Labrador Shelf (Northwest Atlantic) where cod and the majority of other demersal fish declined synchronously in the late 1980s and early 1990s, replaced in dominance in the ecosystem by shrimp and crab (Lilly *et al.*, 2000). In this case, it was likely that environmental change and fishing pressure acted together and likely amplified the affect. During the transition, it was also noted that many of the demersal fish species not only declined but changed their distribution, toward deeper waters (Atkinson 1994). During a similar period, just south of that area, Frank *et al.*, (2005) also reported a shift that they referred to as a trophic cascade on the Scotian Shelf, with a reduction in large demersal fish, including cod and a restructuring of the foodweb. This may be one of the mechanisms that might lead to a regime shift.

It is not clear whether the changes described in the Northwest Atlantic, off Newfoundland and Labrador, and on the Scotian Shelf are all but irreversible but, even with large catch reductions, closures and strict enforcement of limits on many previously dominant commercial fish species, the previous configuration has not been reinstated in almost 20 years. Long established, dominant fisheries have been largely replaced with substantial fisheries for shrimp and crab. Although when originally described, these events were not referred to as regime shifts, the manner in which change occurred fits the description of a regime shift, "a switching between communities" (Steele 2004).

On the other hand, changes in the Northeast Atlantic fish communities, particularly in the seas surrounding Britain comprise distributional shifts, including expansion or contractions rather than full-scale replacement of species assemblages (examples in

ICES, 2008; Corten and Van de Kamp 1996; Beare *et al.*, 2004; Perry *et al.*, 2005; Greenstreet and Rogers, 2006). Climate conditions in the Northwest Atlantic changed (cooled) between the two regimes, a period of cooling (Colbourne *et al*., 1997, Drinkwater 1996) but not to the degree (of warming) that has occurred in the Northeast Atlantic (ICES, 2007) where such a dramatic and abrupt change in demersal community structure has not been observed. Despite greater and longer term changes in water temperature and heavier fishing pressure over a longer period in the Northeast Atlantic, the demersal fish community structure there has not undergone the degree of change that occurred in the Northwest Atlantic. This raises the question of what constituted the ecosystem properties that led to a change in community structure.

Some investigators of ecosystem responses have pursued the idea that there may be substantial differences in the properties of different functional groups present in a system, in terms of their resilience to a changing environment (Steneck, 2001). According to Hughes *et al*. (2005), "this perspective shifts the focus from conservation of targeted (often, commercially important) species to active management of functional groups that support essential processes and sustain ecosystem services, such as fisheries". More diverse systems have a higher probability of functional redundancy and may hence be more resilient (Hughes *et al*., 2005). However, if ecosystem components within the same functional group are similarly sensitive to environmental drivers or disturbance, they will be affected in parallel and consequently not provide additional resilience (Elmquist *et al*., 2003).

Juxtaposing these two situations, northeast vs. Northwest Atlantic may lend some interesting insights into the concept of regime shifts and the sensitivity of different communities and ecosystems. A comparison of four systems, two on either side of the Atlantic: for the Northeast Atlantic, the North Sea (NS, temperate) and the Barents Sea (BS, boreal); for the Northwest Atlantic, the Georges Bank (GB, temperate) and the northeast Newfoundland and Labrador Shelf (ENS, boreal) - reveals that there are striking differences between both the physical and biological environments of some of these systems (App. A).

The ENS has been considered to have experienced an ecosystem regime shift in the early 1990s (Lilly *et al.,* 2000), formerly fish dominated, now crustacean dominated. On the eastern Atlantic side in the BS, also a boreal system, where the fish species composition and some aspects of the physical environment such as bottom temperature are similar, a parallel development has not been observed. The fish in the two boreal systems live in relatively cold and deep waters compared to those in the temperate systems (Appendix A). Consequently, growth-rates of individuals of the same species are expected to be slower in boreal waters. For the temperate GB, although a regime shift was not observed, there have been substantial declines in many demersal fish populations there. In contrast, the North Sea (NS) overall has a similar characteristic community structure for at least 80 years (Greenstreet and Rogers 2006) despite the substantial warming trend there.

While climate variability and change, which includes warming, acidification, and changes in wind and precipitation patterns, are sufficient to exert substantial bottom-up impacts on marine ecosystems, there are often intense pressures from other drivers operating concurrently. These include the effects of fishing, aquaculture, coastal development, eutrophication, pollution (including airborne pollutants), dredging for aggregate extraction and navigation, marine noise, and introduced alien species. Thus the likely response of ecosystems to climate change must be considered in concert with other drivers, and potential additive effects and feedback loops need to be identified. For example, demersal trawling may modify benthic habitat, which has supported a complex ecosystem characterized by functional redundancy to a much simplified habitat and associated community with little redundancy and greater sensitivity or reduced resilience to effects of climate change.

The effects of multiple drivers on marine ecosystems can result in coactive effects and simultaneous changes to different components of the ecosystem. For example, climate change can induce bottom-up effects, affecting temperature and nutrient supply and thus plankton productivity, while concurrent top–down impacts are occurring, for example through predator and biomass removal by fishing (Möllmann *et al*. 2008, 2009). The synergy and interplay between multiple drivers and the dynamic nature of oscillations between bottom-up and top–down controls (Hunt *et al*., 2002, Hunt and McKinnell, 2006) should be the subject of further investigation, especially where hypotheses derived from first principles suggest that the combined effects could result in feedback loops.

If increased productivity and/or diversity act as buffers to regime shifts, there may be less cause for concern about climate-induced regime shifts in areas where diversity and productivity are relatively higher or if climate change negatively affects production and diversity. Primary productivity is a biological variable that we might expect to change most with climate warming, although of course, this will vary among systems. In the Northwest Atlantic, for example, it is expected that further climate warming in the Arctic will lead to greater melting of ice, freshening the waters of and strengthening the Labrador Current (Drinkwater 1996). This would likely increase the impact on primary productivity of the Northwest Atlantic by decreasing temperature and slowing productivity while also creating stronger stratification in the thermo and haloclines which will reduce nutrient availability for surface primary production. One then could expect large changes in productivity and subsequently the fish community of the Northwest Atlantic with climate warming.

7.3.3 Future research directions

At present, we can only speculate on the sensitivity of fish communities to climate-induced regime shifts. What we might ask however, is that with further climate warming, are we most likely to see the largest changes in fish communities in the most northern, boreal or arctic areas. What are the relative importance of diversity and production in terms of system resilience? Predicting what is most likely to occur in the fish community requires an understanding of the physics of the region and physical constraints in regional plankton production.

Further study of the contrasts in physical and biological characteristic and their specific interactions in the four systems compared in App. A may allows us to derive some general hypotheses to gain insights into vulnerability of communities to climate change. Hypotheses to consider may include: (i) Boreal systems are slower in terms of production, growth and reproduction than temperate systems and therefore have a higher sensitivity are less resilient to climate change; (ii) Northwest Atlantic (vs. Northeast Atlantic) systems are lower in diversity and therefore more sensitive to climate change. Another consideration in future studies relates to the axiomatic concept of higher diversity leading to greater stability in the ecosystem (Margalef, 1968). Finally, what other drivers (fishing pressure being a key) must be considered when examining changes in community structure?

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7.5 Appendix A

Table A: Comparison of four systems with respect to components relevant to sensitivity of fish communities to climate change. (Colour-coding: Blue = low, grey = medium, yellow = high).

	NE	NW	NE	NW
	Temperate		Boreal	
	North Sea	Georges Bank/ Gulf of Maine	Barents Sea	Newfoundland Shelf
Regime shift described in fish community of the system overall	No large-scale demersal shift [34, 35]	Yes [15, 30, 32]. but has been linked to fishing activities, as well as climate.	No	Yes [33]
Temperature				
Δ in mean surface T	1.31 °C (1982–2006) [31]	0.23 °C (1982–2006) [31] [23, 24]	0.12 °C (1982–2006) [31] [6]; [27] - temperature anomalies	1.04 °C (1982–2006) [31]
Δ in mean bottom T	1.6 °C (1984–2000) [2]		[27] -temperature anomalies	
Mean annual surface T		[23]	~2.8–4.8 °C (1900–2005) [6] ~2.8–4.8 °C (50–200m depth, 1979–2007) [7, 18]	
Mean annual bottom T	8.6 °C [3]	8 °C [3]	(4 °C– Arcto-Norwegian, [3]) T range: < -1.5 to +7.5 (1998–2006) [10]	2.5 °C [17] T range: -2 to +5°C [D. Kulka, unpubl., data]
Bathymetry				

	NE	NW	NE	NW
	Temperate		**Boreal**	
	North Sea	**Georges Bank/ Gulf of Maine**	**Barents Sea**	**Newfoundland Shelf**
Depth range	Southern NS: < 50 m Northern NS: 50–200 m	Georges Bank: 10 – 300 m	0–800 m [10] Average: 230m Max. depth: 500m (western entrance) Range: 50–200m [27]	0 – 350 m [36]
Productivity (plankton, fish)		High [13–15]	High [5, 19] e.g. capelin: 0.2 g C m-2 yr-1 cod: 0.1 g C m-2 yr-1 [28]	
Diversity				
Species diversity (copepods)	Medium, taxonomic richness: ~ 2–3.5 [4, 12] Diversity higher in southeastern North Sea [35]		Low, taxonomic richness: ~1.5–2 [4]	Low (calanoid copepods) [37]
Species diversity (fish)	Increased [43]	Medium [25]	Low [5]	
Major fish stocks	Atl. Herring *(Clupea harengus)*, sprat *(Sprattus sprattus)*, saithe *(Pollachius virens)*, plaice (*Pleuronectes platessa*), redfish (*Sebastes* spp.), Norway pout *(Trisopterus esmarki)*, sandeel *(Ammodytidae)*, Atl. cod *(Gadus morhua)*, Atlantic mackerel *(Scomber scombrus)*, blue whiting *(Merlangius merlangus)*, sole *(Solea vulgaris)*	Atl. Herring, mackerel, Haddock (Melanogrammus aeglefinus), Atl. cod [40]	Atl. Herring, capelin *(Mallotus villosus)*, Atl. cod, blue whiting [5, 16]	Mackerel, Atl. herring, capelin, Atl. cod, Greenland halibut *(Reinhardtius hippoglossoides)* [41, 42]
Species migrations	Moderate (plaice) [38] to wide (mackerel) [39]		Wide (Capelin) [16] Extensive migrations between Barents and Norwegian Sea (cod, haddock, redfish, herring)	
Resilience				

	NE	NW	NE	NW
	TEMPERATE		BOREAL	
	NORTH SEA	GEORGES BANK/ GULF OF MAINE	BARENTS SEA	NEWFOUNDLAND SHELF
	High in timing of phytoplankton spring bloom [26] Considered possible change in system resilience: [29]			
Other relevant literature on system properties	[20]	[21, 22]	[8], [9], [19], [20]	

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Annex 1:Terms of Reference

a) Explore the utility of a variety of modelling approaches for projecting, decline and recovery of fish community metrics to target indicators of state (e.g. EcoQOs) in response to fishing pressure and environmental variability.

   i) Explore the role of uncertainty (e.g. model, process, estimation, observation uncertainty) in these models in the context of probability of achieving targets.

   ii) Evaluate the potential for and implications of fitting these models to data.

   iii) Explore and update the list of modelling approaches from WGFE 2008, including qualitative modelling.

   iv) Apply models to the North Sea EcoQO.

b) Evaluate metrics to characterize, monitor and detect changes in the structure, function and productivity of fish communities

c) Further develop and explore mapping and other methods for comparing and summarizing fish and fish community distributions in relation to environment and habitat

d) Under the umbrella of abundance/occupancy relationships and essential fish habitat:

   i) Examine abundance occupancy relationships within species, and groups of species in different ecosystems in relation to habitat, environment and anthropogenic impacts

   ii) Compare and contrast abundance/occupancy relationships and life-history characteristics for species common to NW and NE Atlantic (e.g. cod, haddock, spurdog, starry ray and herring)

e) Characterise the fish assemblages associated with offshore habitats (reefs, sandbanks, gas seeps) identified in the EU Habitats Directive.

f) Prepare review papers for the chapters of the ICES position paper on Climate Change on:

   i) Changes in abundance, migration and distributions patterns;

   ii) Sensitivity of marine ecosystems to climate variability and regime shifts

Annex 2: ICES Science Plan Topics

Thematic Area 1: Understanding Ecosystem Functioning

1) Climate change processes, and predictions of impacts
2) Fish life history information in support of EAM
3) Biodiversity and the health of marine ecosystems
4) The role of coastal-zone habitat in population dynamics of commercially exploited species
5) Top predators (marine mammals, seabirds, and large pelagics) in marine ecosystems
6) Sensitive ecosystems (deep-sea corals, seamounts, Arctic areas), as well as rare and data- poor species
7) Integration of surveys in support of EAM

Thematic Area 2: Understanding Interactions of Human Activities with Ecosystems

8) Impacts of fishing with marine ecosystems
9) Carrying capacity and ecosystem interactions associated with mariculture
10) Influence of development of renewable energy resources (e.g. wind, hydropower, tidal and waves) on marine habitat and biota
11) Population and community level impacts of contaminants, eutrophication, and habitat changes in the coastal zone
12) Introduced and invasive species, their impacts on ecosystems and interactions with climate change processes

Thematic Area 3: Development of Options for Sustainable Use of Ecosystems

13) Marine living resource management tools
14) Operational modelling combining oceanographic, ecosystem and population processes
15) Marine spatial planning, including the effectiveness of management practices [e.g. Marine Protected Areas (MPAs)], and its role in the conservation of biodiversity
16) Socio-economic valuation of ecosystem goods and services, and forecasting of the impact of human activities

Annex 3: List of Participants

NAME	ADDRESS	PHONE/FAX	EMAIL
Ken Haste Andersen	The National Institute of Aquatic Resources, Department of Sea Fisheries, Charlottenlund Slot, Jægersborg Alle 1, DK- 2920 Charlottenlund Denmark	Tel: +45 33963375	kha@aqua.dtu.dk
Julia Blanchard	Centre for Environment, Fisheries and Aquaculture Science Lowestoft Laboratory Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK	Tel: +44(0)1502 527701 Fax: +44(0)1502 513865	Julia.blanchard@cefas.co.uk
Tom Blasdale	Joint Nature Conservation Committee, Dunnet House, 7 Thistle Place, Aberdeen, AB10 1UZ UK	Tel: +1224 655708 Fax: +1224 621488	tom.blasdale@jncc.gov.uk
Daniel Duplisea	Department of Fisheries and Oceans, Institut Maurice-Lamontagne, 850 Route de la Mer, Mont-Joli, QC G5H 3Z4 , Canada	Tel: +1 418 775 0881 Fax: +1 418 775 0740	duplisead@dfo-mpo.gc.ca
Jim Ellis (by correspondence)	CEFAS, Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK	Tel: +44(0)1502 524300 Fax: +44(0)1502 513865	jim.ellis@cefas.co.uk
Michael Frisk	Stony Brook University, Stony Brook, NY 11794–5000, USA	Tel: +1 631 632 3750	mfrisk@notes.cc.sunysb.edu
Simon P.R. Greenstreet	Marine Scotland, Marine Laboratory, 365 Victoria Road Aberdeen, AB11 9DB UK	Tel: +44(0)1224 295417 Fax: +44(0)1224 295511	s.greenstreet@marlab.ac.uk
Emma Guirey	Marine Scotland, Marine Laboratory, 365 Victoria Road, Aberdeen, AB11 9DB, United Kingdom	Tel: +44(0) 1224 295439	e.j.guirey@marlab.ac.uk
Ralf van Hal	IMARES, Haringkade 1, PO Box 68, NL-1970 AB IJmuiden Netherlands	Tel: +31 31 7487088	ralf.vanhal@wur.nl

NAME	ADDRESS	PHONE/FAX	EMAIL
Dave Kulka (Chair)	Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St John's, NF A1C 5X1, Canada	Tel: +1 902 2293759 Fax: +1 709 772 5469	Dave.Kulkad@dfo-mpo.gc.ca
Anna Rindorf	DTU-Aqua National Institute of Aquatic Resources Charlottenlund Slot DK-2920 Charlottenlund Denmark	+45 33 96 33 78 +45 33 96 33 33	ar@aqua.dtu.dk
Marie Louise Schroter	DTU-Aqua National Institute of Aquatic Resources Charlottenlund Slot DK-2920 Charlottenlund Denmark		mls@aqua.dtu.dk
Anne Sell	Johann Heinrich von Thunen-Instutute, Institute for Sea Fisheries, Palmaille 9, D-22767 Hamburg, Germany	Tel: +49 40 38905 246 Fax: +49 40 38905 263	anne.sell@vti.bund.de
Stephen Simpson	University of Bristol School of Biological Sciences Bristol BS8 1UG UK	+44 117 954 5909	Stephen.Simpson@bristol.ac.uk
Lorna Teal	IMARES P.O. Box 68 NL-1970 AB IJmuiden Netherlands	+31 (0) 317 487684	Lorna.teal@wur.nl
Verena Trenkel	IFREMER, rue de l'Ile d'Yeu, B.P. 21105, F-44311 Nantes Cedex 03 France	Tel: + 33 240374475 Fax: + 33 240374157	verena.trenkel@ifremer.fr

Annex 4: Agenda

Work days begins 8:30 at ICES HQ

Lunch (12:30 – 13:30)

Day ends ~18:00 to 19:00

Monday, 26 October 2009:

Introductions – Institute, country, interests

Start-up, connection to the server and other logistics will be presented by ICES Staff. An instruction leaflet on how to use the ICES computer system, details on how to connect your laptop to the Secretariat's computer network and other facilities will be provided.

Final formulation of groups for each ToR and assignment of a coordinator who will be responsible for pulling together the corresponding report chapter.

Description of the new ICES Science structure and how we fit in as a group - Dan Duplisea

Presentation on DATRAS (for those not familiar with the system) – Dave Kulka

Other

Tuesday, 26 October 2009:

Group and individual work

Plenary consultation on ToR (a) analysis

Wednesday, 27 October 2009:

Group and individual work

Plenary presentation of work and text

Thursday, 28 October 2009:

Group and individual work

Plenary presentation of work and text

Friday, 29 October 2009:

Group and individual work

Plenary presentation of work and text

Plenary on suggested ToRs for 2009

Compilation of report

Annex 5: Proposed Terms of Reference for the next meeting

The **Working Group on Fish Ecology** [WGFE] chaired by Dave Kulka, Canada will meet in Setè, France, 6–10 September 2010 on:

a) Model the relative effects of climate and fisheries on fish productivity and community structure, including spatial aspects;

b) Review and evaluate metrics to characterize, monitor and detect changes in the structure, function and productivity of fish communities;

c) Develop, explore and apply mapping and other spatial methods for comparing and summarizing fish and fish community distributions in relation to environment and habitat;

d) Examine abundance/distribution relationships within species, and groups of species in different ecosystems in relation to habitat, environment and in relation to anthropogenic impacts;

e) Evaluate fluctuations within fish communities:

i) What constitutes regime shifts in fish communities? Can mechanisms be identified detected?

ii) State changes - Cycles vs. regime shifts

iii) Are anthropogenically induced changes alterable?

Long Term Terms of Reference

Examine climate change processes and predictions of impacts.

WGFE will report by 15 October 2010 (via SSGEF) for the attention of the SCICOM and ACOM.

Supporting Information

Priority:	Link to 2009 Terms of Reference (see Annex 1)

Scientific justification and relation to the 16 high priority topics (hpt) of the Science Plan and Strategic Initiatives (SI)	This ToR is a more general phrasing of the traditional WGFE work on indicators of fish community structure, dynamics, production and function and human and climate impacts. This ToR relates to Science plan theme area 1 particularly, especially high Priority Topics (HPT) points 1,3,4,5. Additionally HPT 8 WGFE is continues to develop and test new community and biodiversity indicators in support of an ecosystem approach to management. ToR B is data part of the modelling work described in ToR a. ToR b therefore in relevant to the same sections of the science plan in addition to HPT 7. This work also has direct relevant to the Strategic Initiative on Biodiversity Objective methods for comparing maps is an essential topic for examining changes in fish distributions in relation to forcing such as climate and fishing effort. Thus, this work could be important in future for SSICC and HPT 1. Sophisticated objective mapping tools are essential in developing strategies for marine spatial planning and therefore relevant to SICZSP and HPT 15. Changes in spatial distribution of fish in relation to external (climate, fisheries, habitat) and internal (density-dependence) forces and the separation of the two remains and important research area in WGFE. This work relates to HPT 2, 3, 5,8,11. This work can provide some theoretical back for work on marine spatial planning especially regarding sensitivity of species groups to habitat destruction and fragmentation with is important for SICZSP. This ToR is an open call to examine the concept of regime shift (and like processes) in marine fish communities. Considerable confusion and contention revolves around this issue currently and WGFE has a range of expertise that may be able to shed light on this work. This work relates to most topics under the Ecosystem Function thematic area and HPTs 8, 16. Because there is considerable interest and expertise on this topic in academia, it is hoped that this ToR may be an incentive for this segment of the research community to attend in greater numbers.
Resource requirements:	
Participants:	The group is normally attended by 15–20 members and guests.
Secretariat facilities:	None.
Financial:	No financial implications.
Linkages to SCICOM steering groups:	SSGEF, SSGSUE, SSGHIE, SSGESST
Linkages to other groups:	Work on simulation in fish communities for the testing of EcoQOs is closely related to the development of multispecies modelling in WGSAM EcoQO work is an important component of advice provided by ACOM The work of this group is an important information source for WGECO (Ecosystem Effects of Fishing) This group has provided key scientific products to the Strategic Initiative on Climate Change (SSICC)
Linkages to other organizations:	Work on indicator modelling and specifically EcoQO projections are the result of OSPAR requests to ICES.

Annex 6: Recommendations

RECOMMENDATION	ACTION
Examine climate change processes and predictions of impacts.	Consider this recommendation when formulating future ToR.

Annex 7: Letter to Position Paper Editorial Team

Chapter 9:

Title: Many comments received suggested broadening the chapter from addressing only the effects of climate change on fish distributions, abundance and migration (as per the original title), to wider effects of climate change on fish populations. As this is the only chapter in the position paper dealing with fish, we decided it was a good suggestion and have adapted the title accordingly. The scope of the chapter has thus been broadened and now extends to climate effects on processes such as growth, survival, recruitment and a section on synergistic effects of climate & fishing, as well as future research needs.

Section 9.2: The original draft dealing with the effects of climate change on fish distributions, abundance and migration has been shortened and inserted in section 9.2. We decided against dividing the section up into the different regions and instead talk more generally about distribution shifts, appearance and colonisation of rare species, and range extensions/retractions using examples from around the world.

We suggest that it may be of value to have an American/Canadian Scientist review this section to ensure enough examples from western areas are included.

Table 9.1: The table is a collation of the tables from the original draft (based on calculations by WGFE 2008). Although it provides a good overview of abundance changes across 4 regions, the table is large. If it is necessary to reduce the size of the table, we suggest using one region as a sample area (text would need no adaptations), or picking up on species differences across different regions (the text above may need some minor adaptation).

Section 9.4: This section has been added due to the large influence of fisheries on fish populations and assemblages which are likely to have a number of interactive effects with climate change. Comments received suggested that Benjamin Planque would write this section, which makes sense (especially based on his current paper in press). The section in its current form is only a rough draft and we would welcome the input of Benjamin Planque. The size of the full Chapter in its current form leaves a reasonable amount of space for an expansion of this section.

Chapter 10:

Some comments received suggested merging chapters 9 and 10, however we agree with comments received from Miguel Bernal: *Chapter 10 is not only about fish, but else about effects in the ecosystem. In this chapter, as Benjamin (Planque) suggested, we will need to deal with trophic effects, changes in energy flow due to changes in climate, changes in ecosystem productivity and composition, etc. I do not think ICES with its ecosystem approach trend can afford to lose this chapter.*

The chapter is thus dealing with ecosystems; however, WGFE has mainly addressed the response of fish within marine ecosystems to climate change, rather than all elements of the marine ecosystem as a whole. **We hope that benthic invertebrate ecologists and biological oceanographers will add in examples from their taxa and realms to diversify the material presented here and form an ecosystem perspective**, but hope the structure of the chapter provides a useful framework within which to work. There should thus be no repetitions from previous chapters but a platform on which examples can be brought together to show effects on and within the ecosystem as a whole. We recommend that this chapter is thoroughly cross-referenced with previous chapters to allow brief reference to taxa-specific patterns in Chapter 10, with more in-depth discussion in the more taxa- or system-focused preceding chapters.

Title: We have dropped fisheries from the title as we feel that it is the interaction of fisheries with climate change that is important for the purposes of this document, not fisheries as a driver in its own right. The interplay of fishing with climate change is discussed in detail in Chapter 9, and touched on in Part C of this chapter in the discussion of multiple drivers.

Other comments received:

Some of the reviewers of the first draft volunteered to write certain sections of the chapters. WGFE welcomes this, as it will improve and extend the knowledge existing within the WGFE.

As suggested above, Benjamin Planque suggested to write (or extend) the section on synergistic effects. Jürgen Alheit has offered to write about *"climatically induced teleconnection patterns in the response of different ecosystems"*, which we suggest can be added into Chapter 10, as well as on some cyclic effects caused by the AMO and/or NAO. Furthermore it was suggested to specifically include the "cod and climate change: initiative of ICES", for which Geir Ottersen was suggested. Geir Ottersen, himself suggested to edit the whole of Chapter 9 together with Miquel Bernal, extending the chapter beyond distribution. As this is already partially done, WGFE suggest they included missing topics. The same for Myron Peck, who volunteered to extend the mechanistic approach by including information on *"climate-driven environmental factors and process-based knowledge"*, specifically on "habitat connectivity" and "direct and indirect impacts" or on physiological thresholds (related to bio-envelope modelling) and impacts of multiple stressors on growth energetics.

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